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ON THE DEVELOPMENT OF THE GENITALIA AND THEIR DUCTS OF ORTHOPTEROID INSECTS

By M. A. H. Qadri, Ph.D. (Aligarh and Cantab.)

(*From the Entomology Department, Zoological Laboratory, Cambridge.*)

Communicated by Dr. A. D. Imms, F.R.S., F.R.E.S.

With Plates 1 to 7.

(Manuscript received 20.iii.1939.).

(Read 7th February, 1940.)

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I. Introduction.

The problem of the genitalia and efferent genital ducts may be regarded as one of the outstanding subjects of insect morphology. A large amount of literature is available on the morphology of the adult organs. Studies dealing with the development of these organs are, however, comparatively few, and the mode of development of the genitalia and efferent ducts in several groups of insects is scarcely well established.

The group known as Orthopteroid insects represents an assemblage of different forms which show a number of generalised morphological features, supposed to be of ancestral type. Walker has included in this group the insects belonging to the Ephemeroptera, Odonata, Plecoptera, Embioptera, Dermaptera, Orthoptera, Isoptera and Zoraptera (a sub-order of Psocoptera). For the first two, namely, Ephemeroptera and Odonata, he, however, concludes that they are circumscribed groups having no near allies among the recent insects. Snodgrass (1937) has included only the Isoptera, Embioptera, Orthop-

tera and Zoraptera among the Orthopteroid insects. Concerning Plecoptera and Dermaptera, he remarks that they appear to be distinct orders having no close relationship with the Orthoptera, since in each of these groups the male reproductive system is specialised in its own way and shows none of the features characteristic of the Orthopteroid insects. The above remark of Snodgrass, though applicable to Dermaptera, does not appear to be wholly applicable to Plecoptera. So far as the development of the male and female genitalia are concerned, my observations reveal a closer affinity of Plecoptera with Orthoptera than is indicated by Snodgrass.

This problem was taken up at the suggestion of Dr. A. D. Imms, to whom I owe a great deal for his many useful suggestions and for the gift of valuable specimens of *Stenoperla*, *Hemimerus* and *Mastotermes*.

For supplying a number of Indian forms, I am very grateful to Dr. M. B. Mizra of Aligarh Muslim University (India). I am also obliged to Mr. G. B. Thompson for his gift of several nymphs and adults of *Hemimerus hanseni* Sharp, to Mr. S. M. Husain of Nagpur University (India) for sending some useful material and to Mr. D. E. Kimmins, Dr. B. P. Uvarov and Dr. L. Chopard for the identification of several forms.

II. Ephemeroptera.

The post-embryonic development of the genitalia and genital ducts was studied in *Chloeon dipterum* (L.), *Ephemera vulgata* L., *Heptagenia* sp., *Rhithrogena* sp., and in *Baetis* sp.

The female.

Adult organs. The female reproductive organs of Ephemeroptera have been described by Palmen (1884), Drenkelfort (1901), Morgan (1913) and more recently by Needham, Traver and Hsu (1935). The following account of *Heptagenia* will illustrate the main features of the genital system in this order.

The ovaries, towards maturity, fill the whole of the abdomen from the second to the seventh abdominal segments. Each consists of numerous ovarioles, arranged along the oviducts. The two ducts run dorso-lateral to the alimentary canal, and in the seventh segment open in close proximity with each other into a shallow cavity or vestibule, between the seventh and eighth sterna (fig. 1, A). Among the other forms studied there is no vestibule, and the oviducts open directly to the outside (fig. 1, B). The vestibule of *Heptagenia* is bounded ventrally by a valve-like intersegmental outgrowth behind the seventh sternum, which has been termed " ovivalvula " by Palmen and " egg valve " by Morgan (fig. 1, A, *egv*). A small sac (*spr*) opens on the dorsal wall of the vestibule in *Heptagenia* and has been regarded as the spermatheca. No female accessory glands are present in any of the mayflies studied, nor are there any traces of the ovipositor on the eighth and ninth sterna.

Development.

The genitalia : Sexes can be distinguished in very young nymphs of Ephemeroptera. In the male nymph the ninth sternum carries the rudiments of the claspers or the styli, while in the female there is no trace of the styli. No rudiments of the ovipositor on the eighth and ninth sterna appear during the post-embryonic development.

The egg valve of *Heptagenia* develops in well-grown nymphs from the

intersegmental region between the seventh and eighth sterna. With the appearance of the egg valve a small space is enclosed between the latter and the openings of the oviduct. This space is regarded as the vestibule.

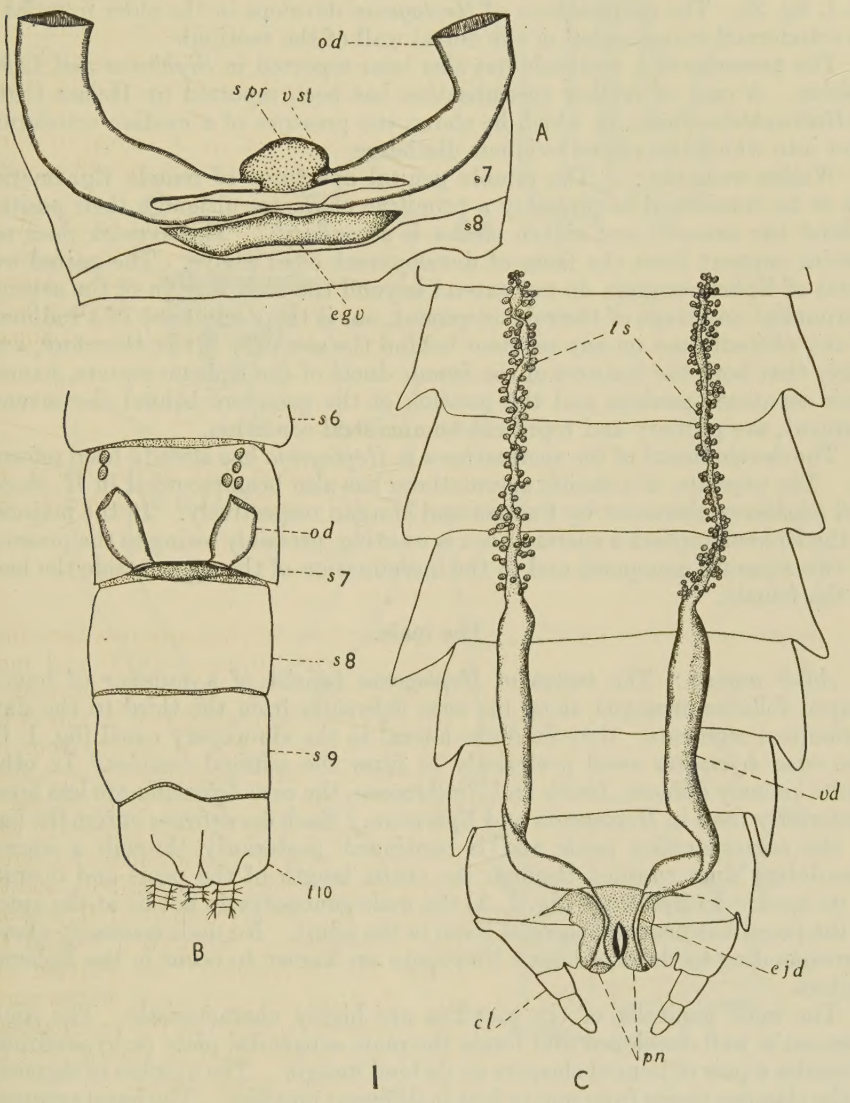

FIG. 1.—A, female genitalia of *Heptagenia* sp. B, female reproductive system of *Baetis* sp. C, male reproductive system of *Heptagenia* sp. *cl*, clasper; *egv*, egg-valve; *ejd*, ejaculatory duct; *od*, oviduct; *pn*, penis; *spr*, spermatheca; *ts*, testes; *vd*, vas deferens; *vst*, vestibule.

A similar egg valve has been described by Palmen in *Heptagenia venosa*, by Morgan in *Siphlurus alternatus* and by Morrison in *Leptophlebia betteni*.

The genital ducts : In very young nymphs of *Heptagenia* and *Rhithrogena*

(pl. 1, fig. 1) the oviducts extend to the hind margin of the seventh segment, where they terminate as ampullae lying far apart from the middle line. During subsequent development the terminal ampullae of the oviducts move towards the middle line and ultimately open directly to the outside (fig. 1, A & B; pl. 1, fig. 2). The spermatheca of *Heptagenia* develops in the older nymphs as an ectodermal invagination of the dorsal wall of the vestibule.

The presence of a vestibule has also been reported in *Siphlurus* and *Leptophlebia*. A case of further specialisation has been reported by Heiner (1915) in *Habrophlebia fusca*, in which he shows the presence of a median ectodermal duct into which the paired oviducts discharge.

Walker remarks: "The double genital apertures of female Ephemerida are to be considered as probably a primitive character although their position behind the seventh and eighth sterna is secondary." This remark does not receive support from the facts of development cited above. The paired oviducts of Ephemeroptera do not extend beyond the hind margin of the seventh sternum at any stage of their development, nor is there any trace of a rudiment of any efferent duct on any segment behind the seventh. It is, therefore, very likely that both the features of the female ducts of the Ephemeroptera, namely their separate openings and the position of the gonopore behind the seventh segment, are primary and represent an ancestral condition.

The development of the spermatheca in *Heptagenia* has already been referred to. The presence of a similar spermatheca has also been recorded in *H. venosa* and *Siphlurus alternatus* by Palmen and Morgan respectively. In the majority of the Ephemeroptera a spermatheca is wanting, probably owing to the presence of two separate gonopores and to the insemination of the eggs outside the body of the female.

The male.

Adult organs: The testes of *Heptagenia* consist of a number of bunch-shaped follicles arranged along the *vasa deferentia* from the third to the sixth abdominal segments; they lie dorso-lateral to the alimentary canal (fig. 1, C). The *vasa deferentia* swell posteriorly to form the seminal vesicles. In other forms, namely *Chloeon*, *Baetis* and *Rhithrogena*, the *vasa deferentia* are less broad posteriorly than in *Heptagenia* and *Ephemera*. Each *vas deferens* enters the base of the corresponding penis and is continued posteriorly through a narrow ejaculatory duct running through the entire length of the penis and opening at its apex. In *Ephemera* (fig. 2, A) the male gonopores do not lie at the apices of the penes but near the bases of them in the adult. No male accessory glands corresponding to those of higher Pterygota are known to occur in the Ephemeroptera.

The male genitalia of the mayflies are highly characteristic. The ninth sternum is well developed and forms the male subgenital plate or hypandrium. It carries a pair of jointed claspers on its hind margin. The number of segments in the claspers varies from one to four in different mayflies. The basal segments are clearly defined from the distal and are provided with muscles. In some mayflies the bases of the claspers are fused in the middle line posterior to the ninth sternum to give rise to a plate termed coxale by Walker.

The penes of Ephemeroptera are paired and tubular outgrowths of the body-wall arising behind the ninth sternum. There are a number of diversities in the shape of the penes in Ephemeroptera, owing to the presence of various accessory structures in relation to them (*vide* Needham, Traver and Hsu). In *Chloeon* the penes are entirely reduced. In others they are well developed

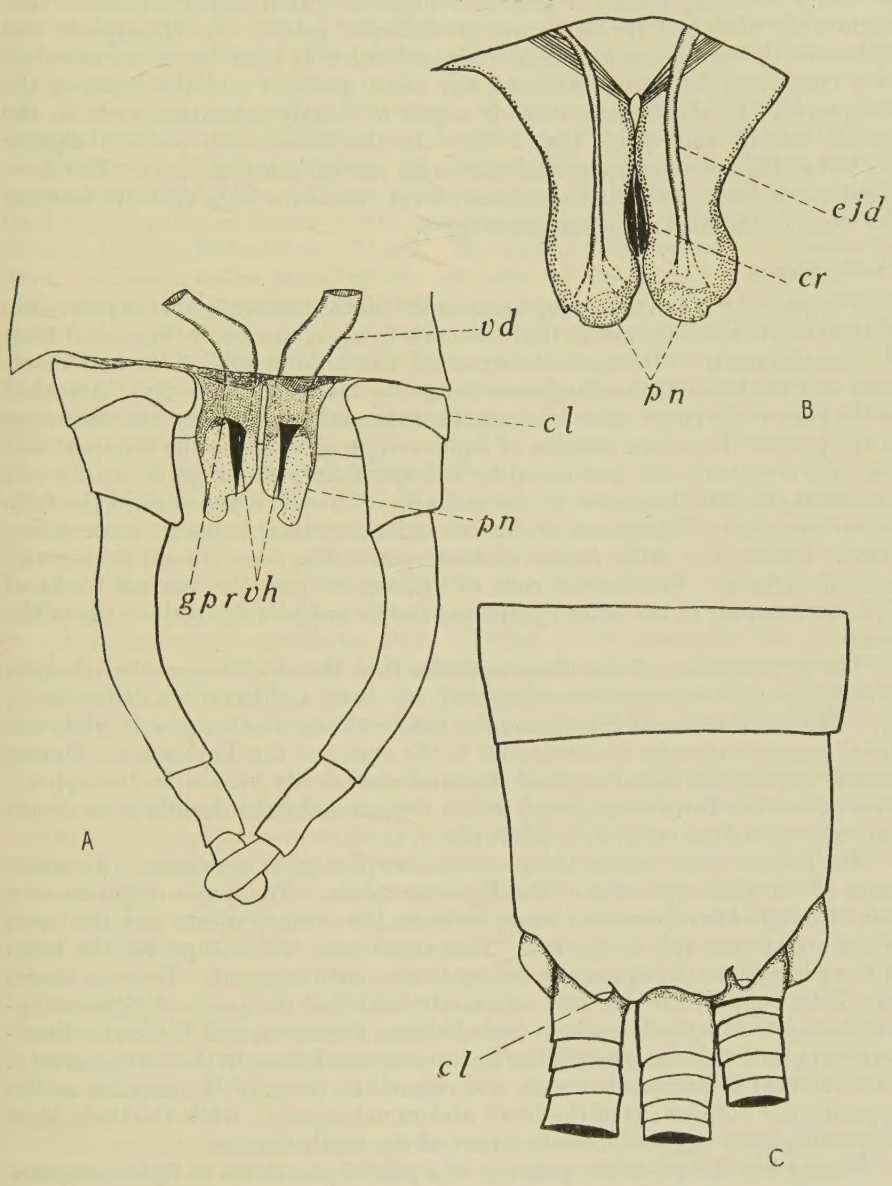

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FIG. 2.—A, male genitalia of *Ephemera vulgata*. B, Penes of *Heptagenia* sp. C, male genitalia of a young nymph of *Heptagenia* sp., 5·5 mm. long. *cl*, clasper; *cr*, chitinous rods; *ejd*, ejaculatory duct; *gpr*, gonopore; *pn*, penis; *vd* vas deferens; *vh*, ventral hooks.

and carry accessory hooks or processes which are often highly sclerotised and immovably attached to the penis at different points. In *Heptagenia* and *Ephemera* the two penes are fused with each other at their bases and attached to a transverse fold lying between the ninth sternum and the bases of the paraprocts. In the former, there is a pair of thickly sclerotised rods on the medial side of each penis (fig. 2, B). In the latter, each penis is slightly bilobed at the apex and carries a hook on its ventral side (fig. 2, A). The short ejaculatory ducts of the last-mentioned form open by a wide aperture between the bases of the hooks and the penes (*gpr*).

Development.

The genitalia : In very young nymphs the ninth sternum bears the rudiments of styli on its hind margin so that the male nymphs can be distinguished from the females easily. The space between the free hind margin of the ninth sternum and the bases of the paraprocts forms the male genital cavity. Attached to the base of the latter there is a pair of ectodermal outgrowths—the rudiments of the penes. In young nymphs of Ephemeroptera the penes lie far apart and are solid structures not perforated by the ejaculatory ducts (pl. 1, fig. 3). In succeeding instars they grow in size and approach each other until in the fully grown nymphs of *Heptagenia*, *Ephemera* and others their bases are more or less fused. During the entire course of development the penes do not betray any sign of division. The medial rods of *Heptagenia* and the ventral hooks of *Ephemera* appear in the older nymphs as simple outgrowths of the walls of the penes.

The development of the claspers shows that the single-segmented claspers of early nymphs becomes two-segmented, one basal and the other distal (fig. 2, C). The basal segment represents the coxite of the ninth segment while the distal segment appears to correspond to the stylus of the Thysanura. During further growth the distal segment becomes secondarily jointed by the appearance of circular furrows or annuli which deepen and subsequently give rise to the segments of the styli of the adult (fig. 1, C, *cl*).

The present observations bring out the morphological significance of various parts of the male genitalia of the Ephemeroptera. The penes originate as a pair of outgrowths from membrane between the ninth sternum and the bases of the paraprocts (pl. 2, fig. 10). This membrane, which supports the bases of the penes, does not appear to belong to the ninth segment. There is, therefore, little support for the view commonly held that the penes of Ephemeroptera belong to the ninth segment (*vide* Palmen, Crampton and Walker). Snodgrass supposed that the penes of the Ephemeroptera belong to the tenth segment. I am inclined to accept that view and regard the penes of the mayflies as the appendicular outgrowths of the tenth abdominal segment, while the basal plate supporting their bases represents a part of the tenth sternum.

Walker has described the presence of a pair of parameres in Ephemeroptera comparable with those of the Thysanura and other insects. Singh-Pruthi (1924), basing his conclusions on the findings of Walker, has compared the parameres of Homoptera with the parameres of *Blasturus* (Ephemeroptera). A semidiagrammatic figure by Walker showing the condition of the male genitalia in Ephemeroptera with the division of each penis into a median and lateral part, has also been incorporated in the modern textbooks. There is no evidence in the development of the mayflies to support the homologies adopted by Walker. The comparison of the parameres of *Blasturus* with those of Thysanura does not appear to conform with the actual facts of development and morpho-

logy. The parameres of the Thysanura belong to the ninth segment and are comparable with the second pair of gonapophyses of the female (*vide* Verhoeff, Heymons and others). The penes and parameres of *Blasturus* and other Ephemeroptera do not belong to the ninth segment at all. The parameres of the Dermaptera and other Pterygota, though essentially different in their nature from those of the Thysanura, are also in no way comparable with those of *Blasturus* or other mayflies. In Dermaptera, and other Pterygota, the parameres arise by the division of the penes or the penis valves into median and lateral parts as shown below, and also described by Christophers, Singh-Pruthi, George, Metcalfe and Sharif. No such division occurs in Ephemeroptera. A comparative study of the genitalia of the nymphs, and adults of different forms of mayflies, shows that the penes, towards the end of the nymphal period, acquire various kinds of hooks and processes attached to them at different points in different forms. These processes and hooks appear to have no morphological significance. They are simply the outgrowths of the penes and occur apparently without any common plan for Ephemeroptera as a whole. The parameres of *Blasturus* appear to be a pair of such processes. Akin to these are the paired medial rods of *Heptagenia* and also the paired ventral hooks of *Ephemera vulgata* L. Needham, Traver and Hsu have made a comparative study of these structures and have classified them into three categories : namely, the parameres, spurs and reflex spurs. According to these authors the above-mentioned structures are of similar nature and occur at different positions in relation with the penes.

It is extremely surprising that Wheeler (1893) compares the penes of Ephemeroptera with the styli of BLATTIDAE (Orthoptera). There is apparently no basis for this homology, since the distal parts of the claspers of Ephemeroptera as shown below are comparable with the styli of Orthoptera (*vide* Crampton, Snodgrass and Imms).

It has been shown above that the jointed claspers of the mayflies represent the appendages of the ninth segment. The basal segment, which alone is provided with muscles, represents the coxite, while the distal segments, which are without muscles and arise by the division of the single distal segment of the claspers of young nymphs, are secondary subdivisions, and collectively represent the styli of the Thysanura and Orthoptera. This view is at variance with that of Walker, who is inclined to regard the terminal segment of the claspers alone as the stylus, and the remaining part as jointed coxite. The post-embryonic development of the claspers of the mayflies as described above does not support the last-mentioned opinion; the views of Crampton and Snodgrass also support the present observations. The last-mentioned author (1936) has fully discussed the nature of the claspers of the mayflies from the morphological standpoint.

The genital ducts : In very young nymphs of *Rhithrogena* and *Heptagenia* the solid strands of the *vasa deferentia* can be traced to the hind margin of the ninth sternum, where they end in hollow ampullae each lying at the base of the corresponding penis (pl. 1, fig. 4). In the early instars the penes are solid and there are no ejaculatory ducts (pl. 1, fig. 3). During succeeding stages the ejaculatory ducts arise as ectodermal invaginations on the dorsal surface of the apices of the two penes (pl. 1, figs. 5 & 6). These ejaculatory ducts traverse the whole length of the penes and establish communication with the ampullae of the *vasa deferentia.* With the further growth of the penes the ejaculatory ducts also increase in their length. In (fig. 1, C) *Heptagenia*, the narrow tubes of the ejaculatory ducts stand in sharp

contrast with the broad terminal ends of the *vasa deferentia*. A chitinous intima extends throughout the length of the ejaculatory ducts, which are quite distinct from the *vasa deferentia* in other histological features as well (pl. 1, figs. 7 & 8). In *Chloeon dipterum* (L.) the penes are reduced, hence the ejaculatory ducts are not fully developed.

The male efferent system of the Ephemeroptera, like that of the female, is also thought to represent a primitive condition. The whole system is paired from end to end and has been regarded by Palmen as the forerunner of the more specialised and terminally unpaired efferent system of higher insects. The last-mentioned author concluded that the entire efferent system of Ephemeroptera is mesodermal in nature. According to him the *vasa deferentia* proceeding backward from the testes enter into the bases of the corresponding penes, and after running through the entire length of the latter directly open to the outside. Palmen further claimed that a chitinous intima does not extend beyond the lips of the openings of the efferent ducts, hence the latter are entirely mesodermal. Wheeler (1893) challenged the views held by Palmen, because he found that a chitinous intima runs deep into the terminal parts of the efferent ducts of *Blasturus*, and is shed off during the nymphal ecdysis. Since studies dealing with the development of the mayflies are extremely insufficient, the views of Palmen have been generally adopted (*vide* Imms, Weber, Needham, Traver and Hsu).

My observations, noted above, do not support Palmen's conclusions. It has already been shown that the efferent ducts of the mayflies consist of two parts, developed quite independently of each other and of wholly different nature. The *vasa deferentia*, in the young nymphs, terminate into hollow ampullae at the base of the penes (pl. 1, fig. 4). There are no ejaculatory ducts in the early nymphs and the penes are solid. During subsequent development an invagination takes place on the dorsal surface of the apex of each penis. This invagination perforates the whole of the penis and communicates with the ampulla of the *vas deferens*. The process of the formation of ejaculatory ducts which takes place in very young nymphs appears to have escaped Palmen's observation, and he probably based his conclusions on the study of the older nymphs. It is, however, surprising that Palmen was unable to mark the exceedingly striking histological differences that exist between the terminal ends of the *vasa deferentia* and the ejaculatory ducts. These differences are especially conspicuous in *Rhithrogena* and (the latter also studied by Palmen) *Heptagenia*, in which the ejaculatory ducts are fairly well developed as compared with those of other mayflies. In all the forms I studied, a chitinous intima is present along the entire length of the ejaculatory ducts, and the denial of its presence by Palmen and more recently by Needham, Traver and Hsu (1935) cannot be accounted for. It may be pointed out that the histological representation of the ejaculatory ducts, given by the last-mentioned authors (pl. 1, fig. 7) is not substantiated by my observations. The ejaculatory ducts are histologically quite different from the *vasa deferentia* and possess an internal lining of chitin and no layer of circular muscles outside as figured by them (pl. 1, figs. 7 & 8).

III. Dermaptera.

The development of the genitalia and their ducts in Dermaptera has been studied in *Forficula auricularia* L. Some nymphs and adults of *Hemimerus hanseni* Sharp are also included in the present observation.

The female.

Adult organs : The ovaries lie dorso-lateral to the alimentary canal. Each consists of a number of ovarioles arranged along the oviducts. The latter unite posteriorly to form a short median oviduct which opens on the venter of the seventh segment. The genital cavity is formed between the posteriorly produced seventh sternum and the membranous eighth and ninth sterna. On the dorsal wall of the genital cavity opens the spermatheca behind the common oviduct. There are no traces of an ovipositor in *Forficula* or in *Hemimerus*.

Development.

The genitalia : In the early nymphal instars of *Forficula* the sexes are difficult to distinguish. In the older female nymphs the seventh sternum is relatively more developed than the eighth and ninth, and helps to separate females from the males. In the first and succeeding instars of *Forficula* no traces of the rudiments of the ovipositor are present. With the growth of the seventh sternum, the eighth and ninth sterna become gradually membranous and telescoped within the former.

The total absence of all the traces of an ovipositor from the development of *Forficula* is a remarkable feature. Crampton, Walker and others hold that the loss of the ovipositor in Dermaptera is a secondary feature, since in the lower Dermaptera (Labiduroidea) a well-developed ovipositor, consisting of two valves, is present. Zacher (1911) has figured an ovipositor in a number of Labiduroidea where it is especially well developed in *Echinosoma* and *Kalocrania*. Crampton (1929) has also figured and described the ovipositor of *E. occidentale* in which the anterior and posterior valves are fully developed. The posterior growth of the seventh sternum appears a characteristic feature of the Dermaptera, in which it forms the female subgenital plate.

The genital ducts : In the first instar nymphs there are no traces of the common oviduct or of the spermatheca. In the succeeding instars two median invaginations can be observed, one on the posterior end of the seventh sternum and the other on that of the eighth. The anterior invagination marks the rudiment of the median oviduct, and on either side of it lie the ampullae of the paired oviducts. The posterior invagination which takes place behind the eighth sternum develops into the spermatheca. During the following growth, the ampullae of the paired oviducts open on either side of the median oviduct (fig. 3, A). The spermatheca (*spr*) becomes slightly convoluted and comes nearer to the median oviduct owing to the reduction of the eighth sternum. There is no trace of a median invagination behind the ninth sternum corresponding to the accessory gland invagination of Orthoptera and other Pterygota.

The male.

Adult organs : The male reproductive organs of *Forficula auricularia* have been described and figured by Meinert (1863), Imms (1934) and others. There is a pair of testes, each composed of two closely applied follicles which are separated from each other towards their blind end (fig. 38). The *vasa deferentia* open posteriorly into a common seminal vesicle (*sv*) which is continued by a median canal—the ejaculatory duct. Near the proximal end of the latter and opening into it, there is a blind pouch (*l.ejd*) which represents the reduced second ejaculatory duct found well developed in *Hemimerus* (fig. 4, A) and many other Dermaptera. Posteriorly the ejaculatory duct of *Forficula* ends in a sclerotised virga which can be everted out of the penis sheath.

The unpaired penis of *Forficula* and *Hemimerus* carries on its sides a pair of parameres (figs. 3 & 4, A, *pm*) which are fused with it at their bases. The male subgenital plate is formed by the ninth sternum which is devoid of any

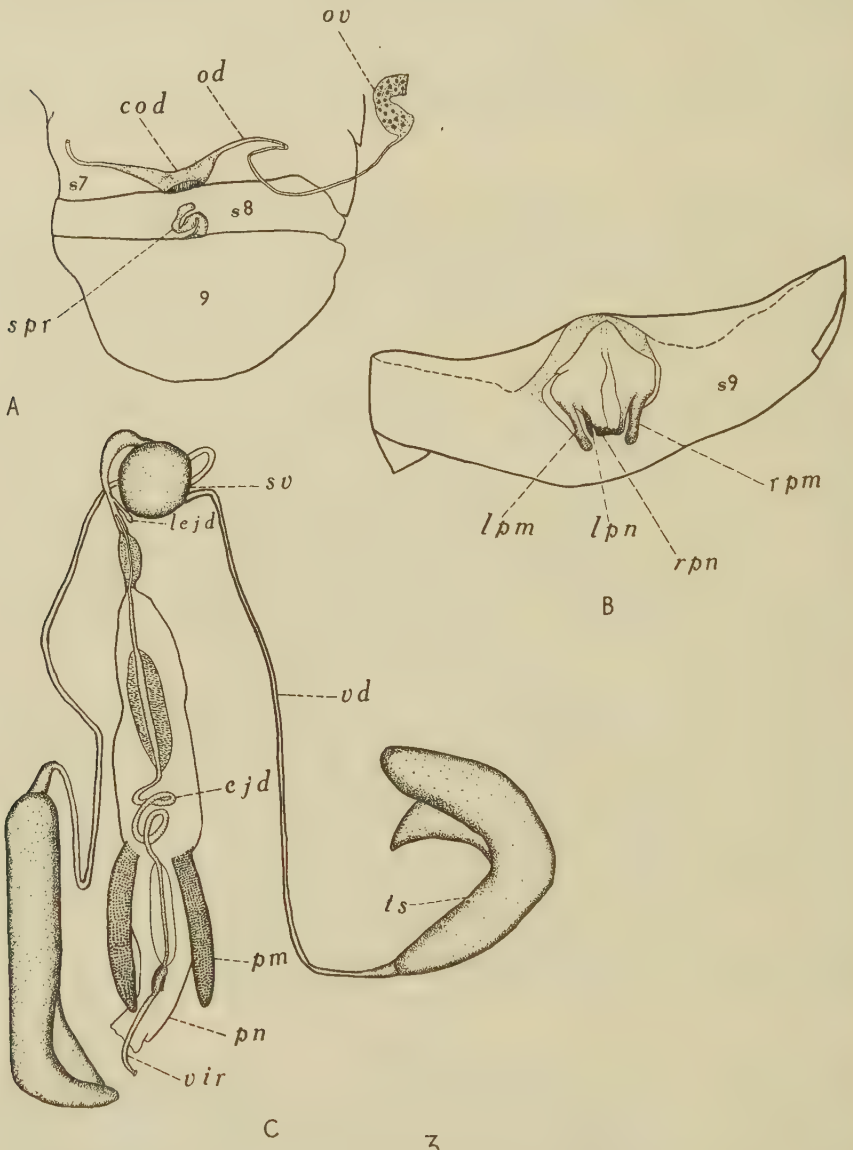

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Fig. 3.—*Forficula auricularia*—A, female reproductive system of a half-grown nymph. B, male reproductive system of adult. C, male genitalia of a full-grown nymph. *cod*, common oviduct; *ejd*, ejaculatory duct; *od*, oviduct; *ov*, ovary; *pm*, paramere; *pn*, penis; *spr*, spermatheca; *sv*, seminal vesicle; *ts*, testes; *vd*, vas deferens; (*l* left and *r* right).

appendicular structures comparable with the styli of Orthoptera and the claspers of Ephemeroptera.

Development.

The genitalia : In the first instar nymphs of *Forficula* the genital cavity is present between the free hind margin of the ninth sternum and the bases of the paraprocts. Inside the genital cavity there is a pair of small ectodermal outgrowths—the penis lobes (pl. 2, fig. 9). They are attached to the base of the genital cavity and lie far apart from each other.

In the third instar, each penis lobe divides at its apex into a median and a

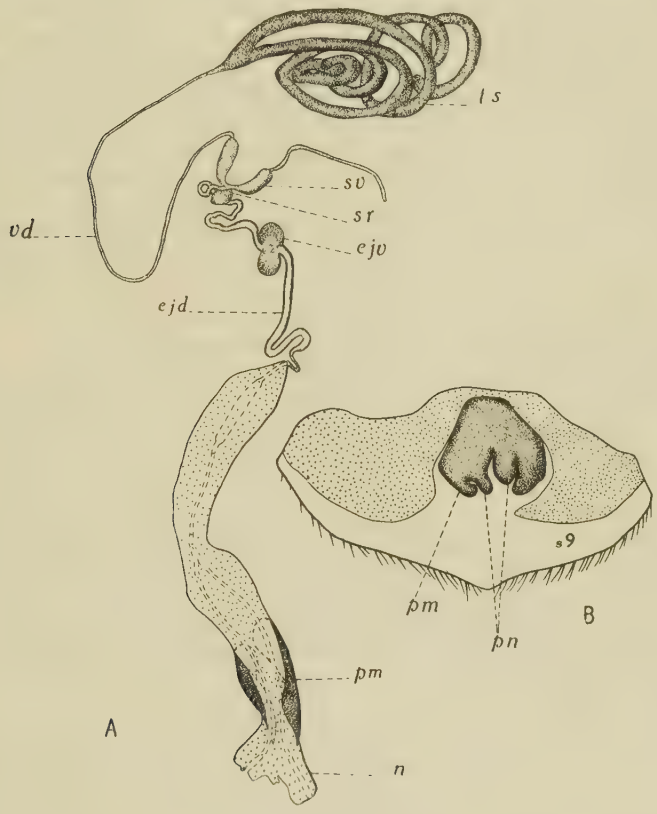

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FIG. 4.—*Hemimerus hanseni*—A, male reproductive organs of adult. B, male genitalia of a nymph 5·5 mm. long. *ejd*, ejaculatory duct; *ejv*, ejaculatory vesicle; *pm*, paramere; *pn*, penis; *sr*, seminal reservoir; *sv*, seminal vesicle; *ts*, testes; *vd*, vas deferens.

lateral part so that the two parts are basally united. The lateral parts are the forerunners of the parameres, while the median ones form the penes. During further development the parameres grow in size and are marked off from the penes. A tendency towards reduction commences in the left penis, while the right one develops quickly and occupies more or less the entire space between the two parameres. In a fully grown nymph (fig. 3, C) the penis of the right side (*rpn*) is enormously developed while the left one (*lpn*) is extremely reduced. In the adults no traces of the left penis can be made out and the median penis

of the adult *Forficula* is, therefore, mainly formed by the right penis of the nymphs. The left and right parameres, unlike the penes, are equally developed.

Throughout the post-embryonic development of the male *Forficula* there are no traces of styli on the ninth segment, nor are there any traces of them in the nymphs of *Hemimerus* (fig. 48).

The above-mentioned development of the penes of Dermaptera suggests a strong resemblance between them and those of the mayflies. Their origin behind and independently of the ninth sternum and the formation of separate gonopores at their apices, furnish a strong evidence in support of the above contention. Snodgrass opposes the idea of a homology between the male organ of Ephemeroptera and Dermaptera on the ground that the latter are basally unpaired, being attached to a median basal plate. It has already been shown that in the first instar nymphs of *Forficula* the two penis lobes lie far apart from each other and are not fused at their bases. The basal plate of the Dermaptera is derived from the wall of the genital cavity and may be compared with the transverse fold supporting the penes of Ephemeroptera. In the Ephemeroptera, there is also a strong tendency for the penes to fuse with each other at their bases, as noted above. A single basal plate has been figured in several Ephemeroptera by Snodgrass (1936) himself, *e.g.*, in *Habrophlebiodes bettoni*, *Campsurus decoloratus*, etc. It is, therefore, doubtful whether the presence of a single basal plate in Dermaptera makes it difficult to homologise the paired penes of Dermaptera with those of Ephemeroptera.

The parameres of *Forficula* and other Dermaptera have been regarded as homologous with the parameres (male gonapophyses of the ninth segment) of Thysanura by Verhoeff, Walker and others. On the other hand, I am strongly opposed to this idea, since the organs referred to above are fundamentally different in their nature and origin in Thysanura and Dermaptera. The parameres of the former (Thysanura) are developed as the medial outgrowths of the coxites of the ninth segment and are homologous with the female gonapophyses. They are entirely separate from the median penis as shown below and as stated by Snodgrass. The parameres of Dermaptera, as noted above, develop from the penis lobes, independently of the ninth sternum. They are fused with the penes at their bases and are not movable, while those of Thysanura are separately provided with muscles and are capable of movement independently of the penis.

The genital ducts: In the first instar nymphs the *vasa deferentia* can be traced to the posterior margin of the ninth segment, where they open into a common seminal vesicle, which appears to have been formed by the fusion of the terminal ampullae of the *vasa deferentia* (pl. 2, fig. 10). There are no ejaculatory ducts in the first instar nymphs. In the next instar each penis is pierced by an ejaculatory duct which is formed by an ectodermal invagination taking place on the dorsal surface of the apex of the penis (pl. 2, figs. 11 & 12). The ejaculatory duct of each penis joins with that of the other and the common duct, which is solid in the earlier stages, extends up to the posterior end of the seminal vesicle (pl. 2, figs. 13, 14 & 15). A chitinous intima continuous with the cuticle of the outside, can be easily detected in the ejaculatory ducts.

During the subsequent development the ejaculatory duct of the left penis is reduced following the degeneration of the latter itself. The reduction of the ejaculatory duct starts first with the loss of the external opening, then gradually proceeds from the posterior end forwards. In fully grown nymphs and even in the adults a trace of the left ejaculatory duct is present in the form of a blind appendage of the right ejaculatory duct as noted above. The virga is

formed by the sclerotisation of the terminal end of the latter, which eventually forms the single ejaculatory duct of the adult.

No male accessory glands are present at any stage of the development of *Forficula*, in which respect it corresponds with the Ephemeroptera.

It is, however, apparent that the efferent system of Dermaptera shows a more specialised condition than that of Ephemeroptera. In the mayflies the male genital ducts, with the exception of *Polymitarcys virgo*, described by Palmen, are entirely separate from each other. In the majority of Dermaptera the terminal ends of the *vasa deferentia* unite with each other to communicate with the unpaired ejaculatory duct formed by the fusion of the anterior ends of the two ejaculatory ducts. This condition appears to have been probably brought about by the fusion of the two penes at their bases. The most primitive condition of the efferent system in Dermaptera is represented by that of *Anisolabis* (Labiduridae). Berlese and Snodgrass have figured the male organs of *A.* [*Borrellia*] *moesta* and *A. maritima* respectively, and have shown that the genital ducts of either sides are entirely separate from each other. This condition very closely corresponds to that of the mayflies, and it seems that in *Anisolabis* neither the *vasa deferentia* nor the paired ejaculatory ducts have united with each other.

IV. Plecoptera.

For the study of the development of Plecoptera, observations were made on *Nemoura variegata* (Oliv.), *Amphinemoura* sp. and *Chloroperla* sp. Some nymphs of *Stenoperla prasina* (Newm.), together with different instars of an unidentified Perlodid, are also included in the present observations.

A. The female.

Adult organs: The female reproductive organs of Plecoptera have been described by Imhoff (1881), Klapálek (1896) and Schoenemund (1912). More recently Wu (1923) has described and figured the female organs of *Nemoura vallicularia* along with a brief account of their development. A characteristic feature of the female organs of Plecoptera appears to be the formation of a loop-like structure which results from the fusion of the anterior ends of the oviducts. The compound female gonad arches over the alimentary canal and a number of ovarioles are arranged along the oviducts running on either side in the body cavity. The whole abdomen is distended with eggs towards maturity. The two oviducts unite posteriorly below the alimentary canal in the seventh segment and form the median oviduct which opens in the genital cavity (fig. 5, A). A highly developed spermatheca is present in the stoneflies and opens on the dorsal wall of the genital cavity. In *Chloroperla*, *Stenoperla* and in the Perlodidae the female genital aperture lies behind the eighth sternum. In *Nemoura* and *Amphinemoura* the genital aperture is situated behind the seventh sternum, and the genital cavity is formed between a special outgrowth of the former and the membranous eighth sternum (fig. 7, A). In *N. variegata* (Oliv.) a bursa copulatrix is also present and opens on the dorsal wall of the genital cavity anterior to the spermatheca (pl. 3, fig. 17).

The recent stoneflies are characterised by the absence of an ovipositor. The ninth sternum is well developed and does not betray any traces of the ovipositor valves. In many Plecoptera the eighth sternum is also well developed, *e.g.*, *Chloroperla*, in which it covers more than half of the anterior part of the ninth sternum (fig. 6, A). In *Chloroperla* the eighth sternum is also devoid of

any traces of the ovipositor valves. In the PERLODIDAE, however, a pair of sclerotised processes border the opening of the genital cavity on the hind margin of the eighth sternum (figs. 5, A & 6, B). Similar structures have also been recorded in PERLIDAE and PTERONARCIDAE.

Development.

Genitalia : In young nymphs of *Nemoura variegata* and *Amphinemoura* a groove runs across the middle line of the eighth sternum. On the posterior

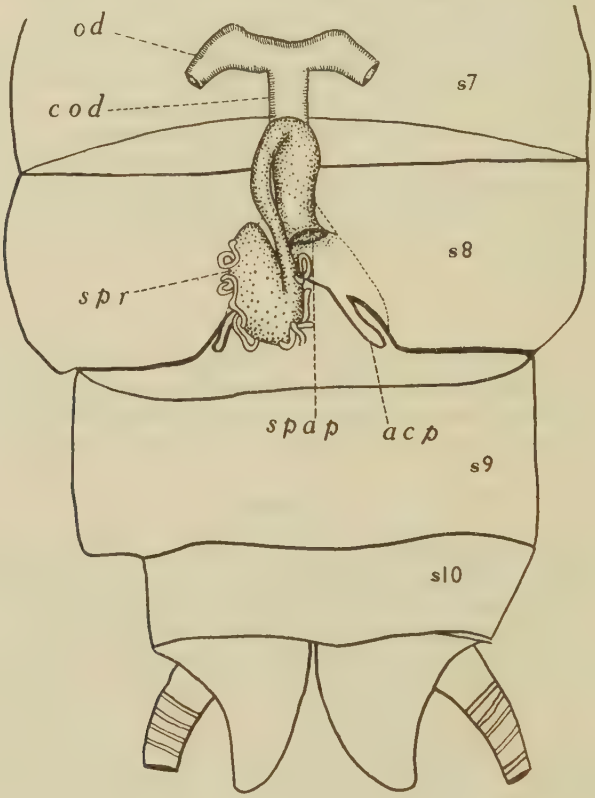

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FIG. 5.—A Perlodid (unidentified)—female genitalia, internal view; *acp*, accessory processes; *cod*, common oviduct; *od*, oviduct; *spap*, spermathecal aperture; *spr*, spermatheca.

end of this groove there is a pair of ectodermal thickenings (pl. 3, fig. 16, *ivl*). The latter lie on the side of the median groove and represent the rudiments of the true anterior valves. During the following stages, the eighth sternum becomes membranous and along with the above-mentioned rudiments of the anterior valves (which do not grow any more), forms the dorsal wall of the genital cavity. Meanwhile the subgenital plate is formed at the posterior margin of the seventh sternum. It grows posteriorly and covers most of the eighth sternum from below (fig. 7, B).

In *Chloroperla* the eighth sternum does not become membranous but, on

the other hand, grows posteriorly to form the subgenital plate referred to above. In the older nymphs of the Perlodid studied, the hind margin of the eighth sternum in the vicinity of the opening of the genital cavity gives rise to a pair of processes. These processes have nothing to do with the anterior valves and develop long after the latter have been incorporated in the dorsal wall of the genital cavity. In a younger nymph of the Perlodid it can also be observed that the hind margin of the eighth sternum is entire and bears no traces of the above processes (fig. 5, B).

No traces of the posterior and lateral ovipositor valves appear during the

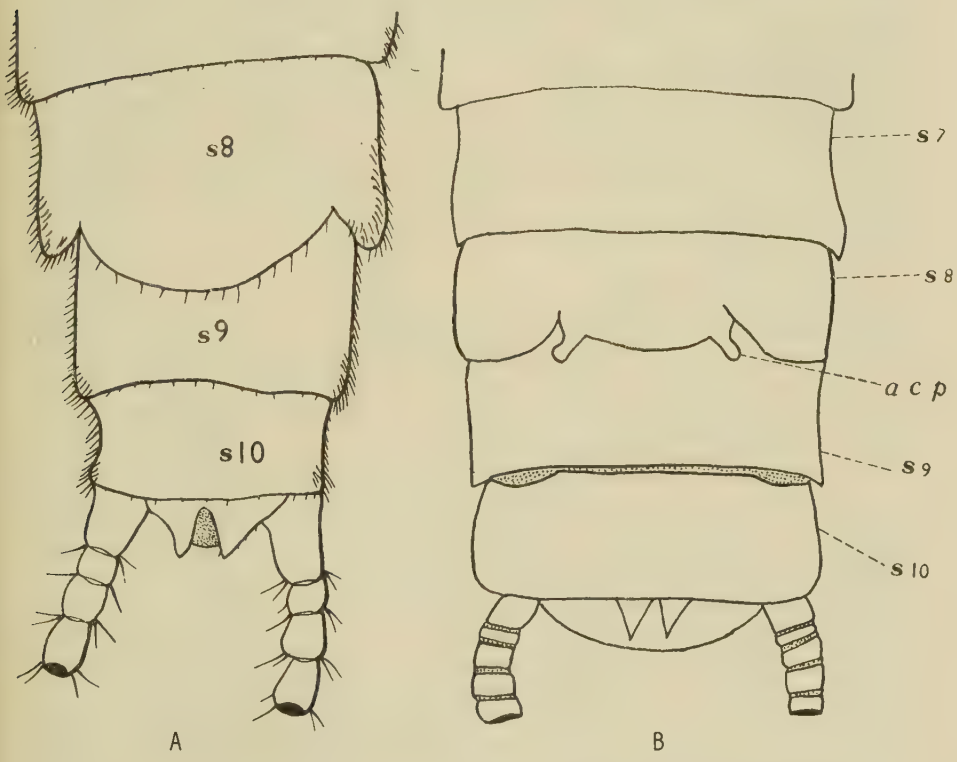

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FIG. 6.—A, ventral view of the abdomen of a female *Chloroperla* sp. B, ventral view of the abdomen of a female Perlodid. *acp*, accessory processes.

post-embryonic development of the forms studied above and the ninth sternum is well developed throughout the nymphal period.

The morphology, as well as the development of the stoneflies studied above, show two distinct types of the female genitalia occurring in Plecoptera. These types, which are especially exemplified by *Nemoura* and *Chloroperla*, will be regarded as 1. Nemourid type and 2. Chloroperlid type in order to elucidate their morphological significance.

In the Nemourid type, as represented by *N. variegata* and *Amphinemoura*, the female gonopore lies behind the seventh sternum, on a subgenital plate formed by the outgrowth of the former. The eighth sternum becomes folded

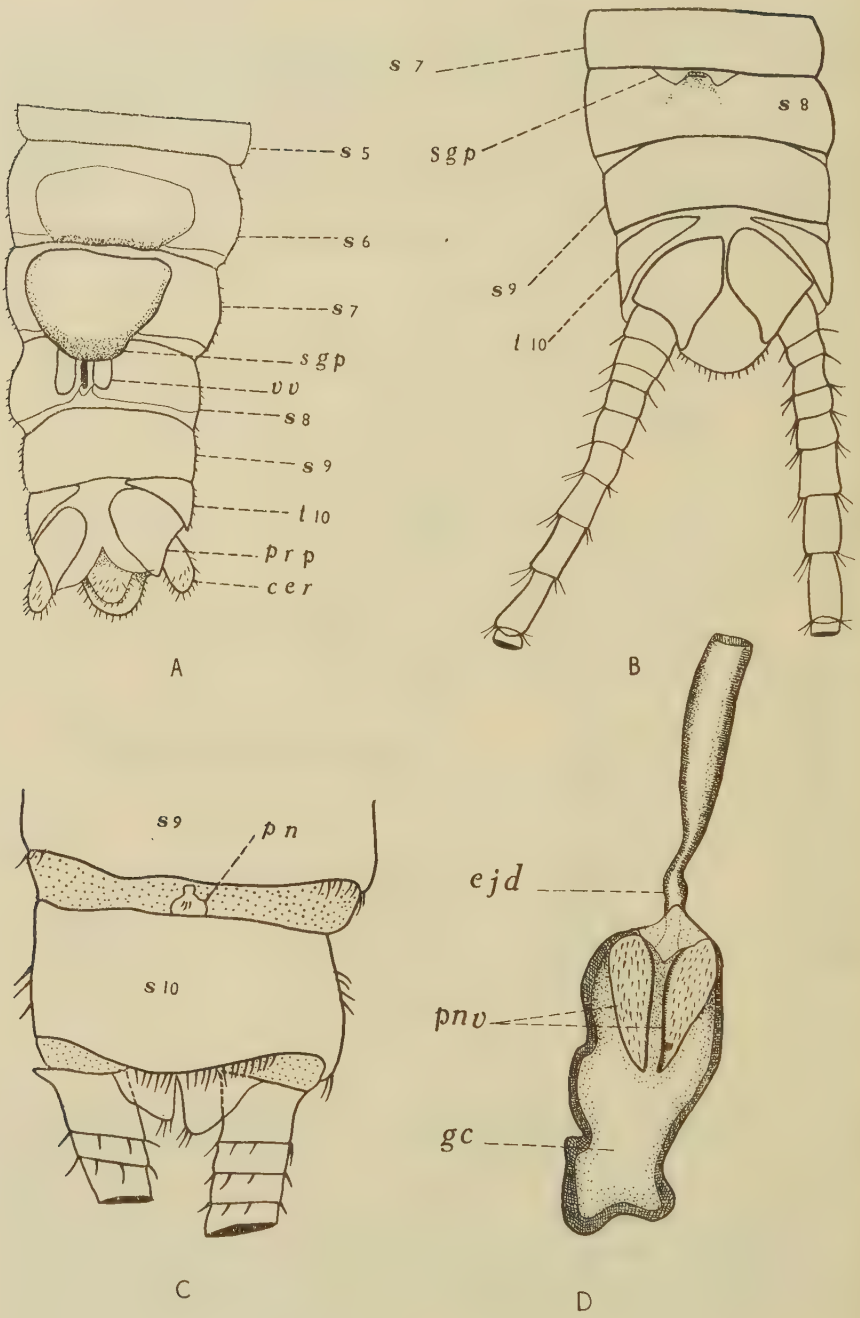

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Fig. 7.—A, ventral view of the abdomen of a female *Amphinemoura* sp. B, same of a half-grown nymph. C, ventral view of the abdomen of a full-grown male nymph of *Stenoperla prasina*. D, male genitalia of *Chloroperla* sp. *cer*, cerci; *gc*, genital cavity; *ejd*, ejaculatory duct; *pn*, penis; *pnv*, penis valves; *prp*, paraprocts; *sgp*, subgenital plate; *vv*, vaginal valves.

and membranous and forms the dorsal wall of the genital cavity. In the Chloroperlid type the female gonopore is situated behind the eighth sternum and the genital cavity is formed between the eighth and ninth sterna. A similar condition is found in *Stenoperla* and in the Perlodid studied.

In *Chloroperla* the eighth sternum grows posteriorly to form a large subgenital plate which is rounded at its hind margin and extends up to the middle of the ninth sternum. In the Perlodid, as noted above, a pair of processes is present on either side of the opening of the genital cavity. Similar processes of the eighth sternum have been reported in *Pteronarcys* by Hagen. Smith and Needham and Claassen have figured and described such processes in a number of PTERONARCIDAE and PERLODIDAE. Walker has interpreted these structures as the rudiments of true anterior valves. Snodgrass is opposed to Walker's idea and regards them as special outgrowths because of their different position from that of the anterior valves. In the Perlodid as noted above, these processes are absent in the young nymphs and arise towards the end of the nymphal life by the modification of the hind margin of the eighth sternum. The rudiments of the true anterior valves are lost following the formation of the genital cavity. These structures are, therefore, evidently secondary structures and do not represent the anterior valves as supposed by Walker.

The genital ducts : In *Nemoura*, *Amphinemoura* and *Chloroperla* the paired oviducts terminate on the hind margin of the seventh sternum (pl. 3, figs. 17 & 18). In young nymphs, two median invaginations appear, one on the hind margin of the seventh sternum and the other on that of the eighth. The invagination, which takes place behind the seventh sternum, grows anteriorly in between the ampullae of the paired oviducts and gives rise to the common oviduct (pl. 3, fig. 19, *cod*). The ectodermal invagination of the eighth segment forms the spermatheca (pl. 3, figs. 16 & 19, *spr*).

The further process of the development of the female genital ducts is different in NEMOURIDAE and *Chloroperla* (PERLIDAE). In *N. variegata* and also in *Amphinemoura* the eighth sternum becomes membranous and telescoped inside the subgenital plate which is the posterior outgrowth of the seventh sternum. The genital cavity of these forms is, therefore, formed between the seventh and eighth sterna, and the female gonopore is situated behind the seventh sternum. The spermatheca, as stated above, opens on the dorsal wall of the genital cavity. In *N. variegata* a bursa copulatrix is also developed from the dorsal wall of the genital cavity and opens at its anterior end. In *Chloroperla* and in the Perlodid, the common oviduct extends to the posterior margin of the eighth sternum (pl. 3, fig. 18, *cod*). The posterior extension is brought about by the formation and subsequent closure of a groove on the venter of the eighth abdominal segment. The sides of this groove close dorsally from the anterior towards the posterior end (pl. 4, fig. 29).

My findings in *Nemoura* and *Amphinemoura* are in agreement with those of Wu, who in *N. vallicularia* also stated that a median invagination behind the seventh sternum forms the vagina. Wu's description of the development of spermatheca and bursa copulatrix is not supported by my findings. According to him, the spermatheca and bursa copulatrix are also formed by the invagination of the vagina. It appears that Wu has probably overlooked the earlier development of these structures, since his studies seem to be based on fairly well-grown nymphs.

In very young nymphs the median invagination of the eighth segment which gives rise to the spermatheca can be clearly distinguished from that of

the seventh segment which forms the median oviduct (pl. 3, fig. 19, *spr*, *cod*). The bursa copulatrix, which is present only in some species of *Nemoura* and absent in a number of others as well as in *Amphinemoura*, develops as a special outgrowth of the dorsal wall of the genital cavity.

The efferent system of the " Chloroperlid " type is to be distinguished from that of the " Nemourid " type, especially by the fact that the common oviduct opens behind the eighth sternum. The posterior extension of the common oviduct from the hind margin of the seventh sternum to that of the eighth is brought about by the formation and subsequent closure of an ectodermal groove along the middle line of the latter. A similar condition appears to exist in *Stenoperla prasina* Newm. and in the Perlodid I studied.

Crampton (1917) holds that in Panplecoptera (Plecoptera and Embioptera) the lack of an ovipositor and styli may be regarded as a retention of primitive condition rather than one brought about by the loss of these structures. This statement, so far as the Plecoptera are concerned, does not receive any support from my observations, since the rudiments of the anterior valves have already been shown to appear in the young nymphs of various Plecoptera.

The male.

Adult organs : The male reproductive organs of Plecoptera have been described and figured by Klapálek and Schoenemund. More recently Mertens (1923) has figured the adult male organs of *Leuctra prisma*, and Wu has described the male organs of *Nemoura vallicularia* together with a brief account of their post-embryonic development.

In *N. variegata* the testes consist of fourteen follicles. The *vasa deferentia* run towards the posterior end of the body cavity. In the hind region of the ninth segment they take a sharp bend and run towards the head to open in the anterior end of the ejaculatory duct. The latter is a fairly long and broad tube and opens posteriorly between the ninth and tenth sterna (pl. 3, fig. 20). There are no male accessory glands in the forms I studied. Two pairs of male accessory glands are present in some stoneflies, *e.g.*, *Isopteryx tripunctata* as described by Klapálek.

No true penis is present in *Nemoura* and *Amphinemoura*. Secondary structure in the form of grooves, hooks and processes are developed especially on the epiprocts and paraprocts, and have been described in detail by Klapálek, Crampton, Walker and others. In *Chloroperla* an eversible penis is present. It is fully developed, bilobed and lies retracted in the genital cavity formed between the ninth and tenth sterna (fig. 7, D).

The male subgenital plate is formed by the ninth sternum which is highly and differently modified in various forms. In *Chloroperla* it assumes a form more or less resembling the subgenital plate of Acrididae (Orthoptera). The tenth sternum is well developed in a number of stoneflies (fig. 7, C).

Development.

The genitalia : In *Nemoura* and *Amphinemoura* all traces of the penis are absent from the entire post-embryonic development. In very young nymphs there is a median invagination behind the ninth sternum, which grows anteriorly and forms the ejaculatory duct. In older nymphs the paraprocts and epiproct acquire secondary structures referred to above.

In *Chloroperla* the genital cavity is formed between the ninth and tenth sterna and is produced anteriorly in the form of an elongated and wide tube.

On the anterior end of the genital cavity there is a pair of outgrowths—the penis valves, each of which in the older nymphs is divided by a horizontal cleft into the dorsal and ventral valves (pl. 3, figs. 21, 22 & 23). These penis valves in their form and position are comparable with the penis valves of Orthoptera described below. The opening of the median ejaculatory duct is located between their bases. Towards maturity the wall of the genital cavity is thrown into a number of folds and several sclerotised ridges are found lining it internally.

The study of the male organs in the above stoneflies also shows two types, as in the female, namely the Nemourid type and the Chloroperlid type. In the Nemourid type the development of *Nemoura* and *Amphinemoura* clearly shows the absence of a true penis comparable with the copulatory organs of other Pterygota. The transference of the sperms is apparently brought about with the help of accessory processes which arise in connection with the epiproct and the paraprocts. Wu's findings in *N. vallicularia* support the above observations, Klapálek's figures and description of the male organs of several species of *Nemoura*, including *N. variegata*, also show the absence of penis in these forms. Crampton, however, reports the presence of a bipartite sclerotised penis in *N. completa*. In my opinion, the structures described and figured by Crampton do not represent a true penis and are probably accessory structures formed at the bases of the paraprocts. Wu in *N. vallicularia* also describes how during the final moult, such copulatory hooks are formed inside the triangular subanal lobes (paraprocts). In *Chloroperla* a true penis is present, which is eversible and lies concealed at the base of the genital cavity. It consists of a pair of penis valves, which, as regards their form and position, resemble those of Orthoptera. The penis valves of *Chloroperla* are divided into dorsal and ventral parts corresponding to those of Orthoptera and likewise enclose the opening of the median ejaculatory duct between their bases. Palmen (1884) in his schematic figure of *Perla bicaudata* shows the formation of the penis by a pair of penis valves. Snodgrass (1936) in *Acroneura arida* has also described and figured a membranous, bilobed and eversible penis, which he terms a phallus, comparable with the median intromittent organ of higher Pterygota. Needham and Claassen in *A. pacifica* and in *Perlodes*, and Crampton in *A. brevipennis* and in *Perlesta placida*, have also figured a fairly well-developed and eversible penis.

The important morphological differences found between Nemouridae and other Plecoptera described above have been overlooked by most workers. It is, however, very difficult to decide whether the loss of the penis in Nemouridae is a primary or secondary feature. The absence of styli from the ninth sternum of all the Plecoptera is also a feature characteristic of this group.

The genital ducts : The *vasa deferentia* in all the forms studied meet the posterior end of the ninth segment and end into swollen ampullae communicating with the anterior end of the ejaculatory duct. With the anterior growth of the median ejaculatory duct, especially in Nemouridae, the point of the union of the *vasa deferentia* and the median ejaculatory duct is carried more anteriorly, with the result that in the full-grown nymphs and adults the *vasa deferentia* take a sharp bend in the ninth segment and run anteriorly on either side of the median ejaculatory duct. No male accessory glands are present at any stage of the development of the stoneflies studied.

In *Chloroperla* the male ducts develop in a manner fundamentally identical with that of *Nemoura* and *Amphinemoura*. The only difference is that the *vasa deferentia* in *Chloroperla* unite at their terminal end to form a short meso-

dermal duct which posteriorly becomes continuous with the median ejaculatory duct.

V. Orthoptera.

1. Blattidae.

The following observations on Blattidae are based on the development of *Blatta orientalis* L. and *Periplaneta americana* (L.). Since these forms agree to a large extent in the main features of the development of their genitalia and genital ducts, the following description will be chiefly based on *B. orientalis* with occasional reference to *P. americana.*

The female.

Adult organs : The ovaries lie in the body cavity in the third to fifth abdominal segments. Each consists of eight ovarioles held together at their anterior ends. The paired oviducts are short and broad and unite below the alimentary canal in the seventh segment to open at the base of a semicircular plate which is concealed beneath the enormously grown seventh sternum. The above-mentioned plate has been termed " vaginal plate " by Vogel and " epigyne " by Chopard, and according to Denny, Chopard, Vogel and Nel, represents an intersegmental outgrowth between the seventh and eighth sterna. Walker, Ford and Snodgrass, on the other hand, regard this plate as a reduced eighth sternum. A discussion regarding its nature will follow elsewhere. The seventh is the last visible sternum and is very greatly enlarged. Its hind margin is medially cleft in order to form a pair of valve-like structures which hold the ootheca during its passage to the outside.

The space enclosed by the enlarged seventh sternum should not be regarded as the genital cavity. The true genital cavity lies between the united bases of the anterior valves of the ovipositor and the subgenital plate or the vaginal plate referred to above. The bilobed spermatheca opens by means of a median aperture on the dorsal wall of the genital cavity, in front of the opening of the common oviduct, and further behind, the median aperture of the colleterial glands lies between the bases of the posterior ovipositor valves.

The ovipositor of *Blatta* (fig. 8, A) is fairly developed though not exserted like that of saltatorial Orthoptera. It consists of three pairs of valves : viz., the anterior, posterior and lateral valves. In addition to these genital valves there is a number of accessory sclerites forming the roof and the sides of the genital cavity which have been fully described by Miall and Denny, Walker, Chopard, Vogel and, more recently, by Snodgrass.

The genitalia : In the first instar nymphs the sexes cannot be easily distinguished, and the ninth sternum in both the sexes carries posteriorly a pair of well-developed styli. On closer observation, the female nymphs can be distinguished from the male nymphs by the presence of a minute median notch on the posterior margin of the ninth sternum. The above-mentioned notch divides the hind region of the ninth sternum into two parts each carrying a stylus on it. Each of these parts, as shown below, represents the rudiments of the lateral valves. The posterior valves are not developed at this stage. The eighth sternum in the first instar nymphs consists of a narrow band which is weakly sclerotised, especially in the middle, and does not bear any traces of the styli as does the ninth. A transverse section passing through the posterior margin of the eighth sternum shows that the latter is also cleft in the middle like the ninth sternum. The above-mentioned cleft of the eighth sternum

divides the posterior region of the latter into two parts which correspond to those of the ninth (pl. 4, fig. 24).

It might be pointed out here that Nel in *Blattella germanica* figures and describes a similar condition. He, however, interprets the bilobed posterior part of the eighth sternum as anterior valves, thus homologising them with the lateral valves of the ninth segment. This interpretation is incorrect, since the structures referred to simply represent the bases of the anterior valves or the coxites of the eighth sternum from which the anterior valves arise during the

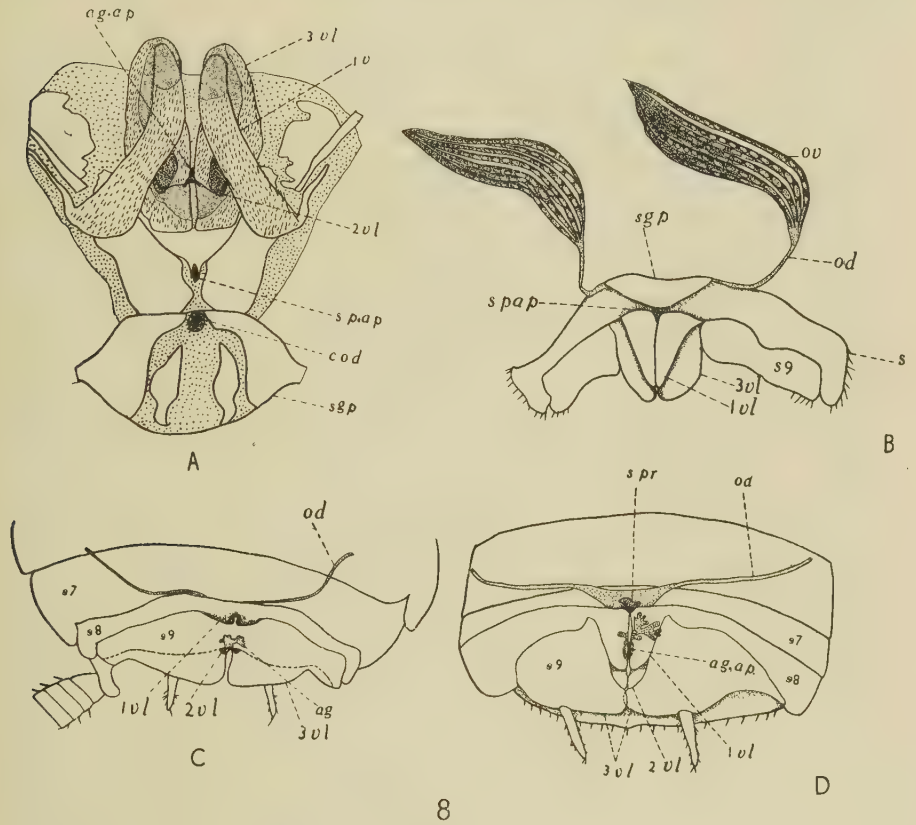

FIG. 8.—*Blatta orientalis*—A, female genitalia. B, ventral view of the female genitalia of sixth instar nymph. C, internal view of the female genitalia of the third instar nymph. D, same of the fourth instar nymph. *ag*, accessory glands; *agap*, accessory gland aperture; *cod*, common oviducal aperture; *od*, oviduct; *ov*, ovary; *sgp*, subgenital plate; *spap*, spermathecal aperture; *spr*, spermatheca; *vl*, ovipositor valves.

subsequent development. It may, therefore, be pointed out that during the early part of the nymphal life the coxites of the eighth and ninth segments are alone differentiated, while the anterior and posterior valves arise from them some time later during the following nymphal growth. Denny in *Blatta* also refers to the absence of the anterior and posterior valves during the first and second stadia.

In the second instar no important change occurs in the genitalia and the anterior and posterior valves are still undeveloped. The median cleft of the

ninth sternum, however, deepens so as to mark the formation of the dorsal ovipositor valves.

In the third instar the posterior valves make their appearance on either side of the base of the median cleft and thus appear to be median outgrowths of the latter (fig. 8, C, 2*vl*). The anterior valves also appear in the same instar as outgrowths of the coxites of the eighth segment on either side of the median cleft (1*vl*). The figure (pl. 4, fig. 25) of the transverse sections passing through the eighth sternum clearly shows that the anterior valves are not simply modified coxites like the lateral valves but arise by the division of the coxite by a vertical groove.

During the second and third stadia the eighth sternum becomes membranous and is telescoped within the seventh. Meanwhile a small fold grows from the intersegmental region between the seventh and eighth sterna and in the third instar it becomes a small semicircular plate lying above the seventh sternum. This semicircular plate represents the rudiment of the subgenital plate which in the adult carries the gonopore on it, as stated previously.

The further development shows the growth and modification of the structures already mentioned (fig. 8, D). The lateral valves become modified to assume their true form and the styli borne by them are cast off during the last nymphal stage (fig. 8, B). The posterior valves also grow in size, and so do the anterior valves which form the ventral shafts of the ovipositor and become movably articulated with their bases or the first pair of valvifers, which according to Snodgrass also represent the coxites of the eighth segment. The eighth sternum becomes membranous and most of it lies concealed beneath the seventh sternum. The mode of development of the above-mentioned genital structure in *Periplaneta* is similar to what has been described above in *Blatta*.

The genital ducts : In the newly hatched *Blatta* the paired oviducts can be traced to the hind margin of the seventh sternum, where they terminate into ampullae which lie on either side of the middle line (pl. 4, fig. 26). An ectodermal thickening on the hind margin of the seventh sternum forms the rudiments of the median oviduct and the ampullae of the paired oviducts lie on either side of it. A median invagination on the posterior margin of the eighth sternum marks the origin of the spermatheca and another median invagination behind the ninth sternum is the forerunner of the colleterial glands.

In the succeeding instars the ectodermal rudiment of the median oviduct assumes the form of a short duct into the anterior end of which open the ampullae of the paired oviducts. The growth of the subgenital plate results in the posterior extension of the common oviduct brought about by the formation of a dorsal ectodermal groove and by the subsequent closure of its upper surface (pl. 4, fig. 27). The spermatheca (*spr*) develops from the invagination of the hind margin of the eighth sternum and opens between the bases of the anterior valves. During further growth it assumes a tubular shape and becomes coiled. The median invagination behind the ninth segment gives rise to the female accessory glands. They open between the bases of the posterior valves by a short median duct immediately bifurcating into two branches which further branch and sub-branch and give rise to the colleterial glands.

The male.

Adult organs : The male reproductive organs of *Blatta orientalis* have been described and figured especially by Miall and Denny among the earlier workers. Quite recently Snodgrass (1937) has described the male organs of *Blatta*, *Periplaneta* and other Blattidae in detail. In a young adult *Blatta* the testes

consist of a pair of bodies formed by a number of ovoid follicles arranged along the anterior ends of the *vasa deferentia*. Each *vas deferens* of the adult is a short but comparatively stouter tube, and branches to join again at two places during its course towards the posterior end. The *vasa deferentia* open in the anterior end of the ejaculatory duct along with a large number of accessory glands which have been termed " utriculi " by Miall and Denny and are also collectively known as " mushroom-shaped gland." They have been grouped into two sets by the above-named authors—one consisting of the median short tubes and the other of longer and peripheral tubes. There is, however, another set of about nine small vesicles on each side of the ventral surface of the anterior end of the ejaculatory duct, which store the spermatozoa and may be termed seminal vesicles (also *vide* Snodgrass, 1937).

The conglobate gland is a fairly well-developed gland of unknown function and opens independently of the ejaculatory duct between the dorsal and ventral parts of the left penis valves.

The male subgenital plate or the hypandrium is formed by the ninth sternum which carries a pair of styli at its hind margin. Above the hypandrium lies the inner part of the male genitalia which apparently consists of a series of hooks and processes. These structures of *Blatta* and *Periplaneta* have been more recently described and figured by Chopard (1920), Walker (1922) and by Snodgrass (1935–37). It is, however, unfortunate that all the above-mentioned authors are in great disagreement regarding the interpretation of the different structures, and all three have employed different terminology for them. In the present work Chopard's terminology has been adopted with certain necessary modifications, since in my opinion his scheme is more in accordance with the fundamental nature of the inner parts of the male genitalia.

The inner male genital structures of adult *Blatta* consist primarily of two pairs of lobes which are arranged round the male gonopore and represent the subdivisions of originally a single pair of right and left penis valves (fig. 9, A). The right dorsal and ventral penis valves are easily distinguished from each other, since they lie far apart, the former dorsal to the gonopore and the latter ventral to it. The left ventral and dorsal penis valves are more or less fused with each other at their bases and have been displaced from their original position due to the asymmetrical development of the male genitalia, which is a characteristic feature of Blattidae. The combined left dorsal and ventral valves lie on the left side of the male genital aperture. Snodgrass refers to the right dorsal penis valves as left phallomere. Walker, on the other hand, refers to the latter as sinistral paramere and to the right dorsal penis valve as dextral paramere, and to the left ventral penis valve as penis. It may be pointed out that in *Blatta* and *Periplaneta* a true penis or an intromittent organ, comparable with that of other insects, is not present independently of the above-mentioned structures, and the membranous terminal part of the ejaculatory duct may be referred to as a functional penis. Chopard also designates a process of the left penis valve as penis, but, as mentioned above, this is not in accordance with the true facts of morphology.

Development.

The genitalia : In the just-hatched nymphs of the cockroach, the ninth sternum is well developed. It is rounded on its posterior margin and carries a pair of styli. The genital cavity is formed between the free hind margin of the ninth sternum and the membranous tenth sternum which is fused with the

bases of the paraprocts (pl. 4, fig. 28). At the base of the above-mentioned genital cavity there is a pair of ectodermal outgrowths which lie one on either side of the middle line (pl. 4, fig. 29). These paired outgrowths are the forerunners of the inner part of the male genitalia and may be termed penis valves, since they appear to be comparable with the rudiments of the copulatory organs of other Pterygota termed penis valves or penis lobes by Crampton,

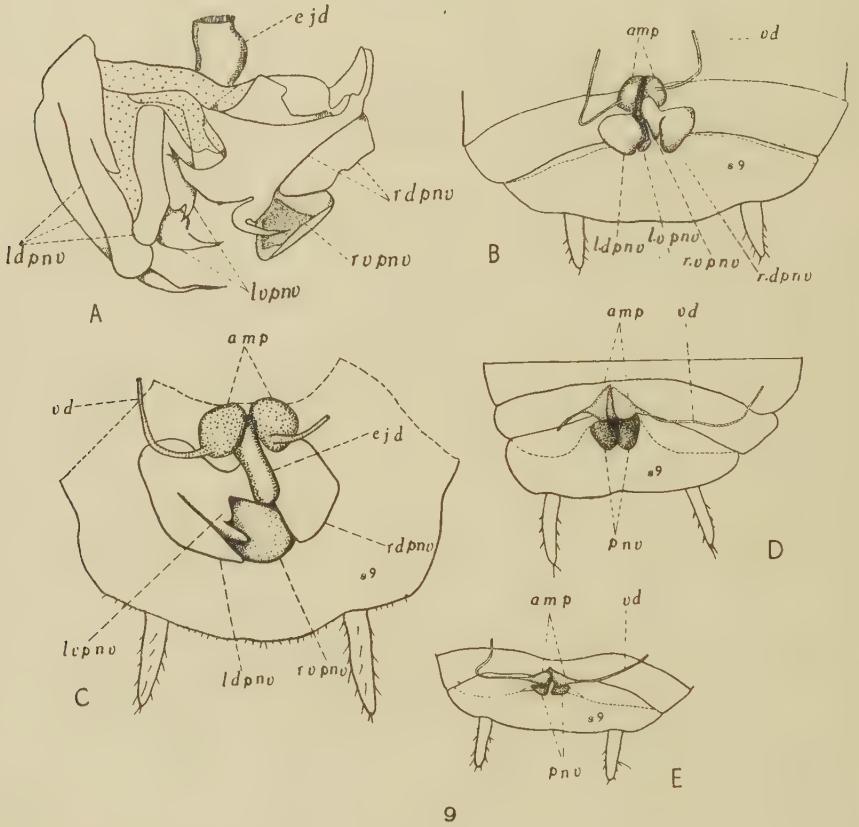

Fig. 9.—A, male genitalia of *Blatta*. B, same of fourth instar nymph. C, same of sixth instar nymph. D, same of second instar nymph. E, male genitalia of second instar nymph of *Periplaneta americana*. *amp*, ampullae of the vasa deferentia; *ejd*, ejaculatory duct; *pnv*, penis valves; *vd*, vasa deferentia; (*l*, *r*, *v* and *d*, left, right, ventral and dorsal).

Chopard, George, Metcalfe, Else, Sharif and others. Between the bases of the penis valves there is a median invagination which is the rudiment of the median ejaculatory duct. An asymmetry of the penis valves is apparent, especially in *Blatta*, from the first instar and the median ejaculatory duct runs along an oblique course forward.

In the second instar no important change occurs in the structures mentioned above beyond a general growth (figs. 9, D & E).

In the third instar each penis valve divides by means of a horizontal fissure into dorsal and ventral parts (pl. 4, fig. 30), so that there are now four penis valves which surround the opening of the ejaculatory duct.

In the succeeding instars the development of the male genitalia consists chiefly of growth and modification of the above-mentioned structures (fig. 9, B & C). The right dorsal penis valve becomes dorsal to the male genital aperture and develops a number of accessory hooks and processes. The right ventral penis valve moves down below the gonopore and remains simple. A complication is, however, introduced in the subdivisions of the left penis valve with the consequence that the dorsal and ventral parts of it are not so well demarcated as the right dorsal and ventral penis valves.

It may be pointed out that Snodgrass traces the inner part of the male genitalia of *Blatta* and *Periplaneta* from three rudiments which he terms left, right and ventral phallomeres, and regards as special outgrowths of the genital cavity peculiar to Blattidae. While a discussion of the nature and homologies of the penis valves will appear elsewhere in the present work, it may be observed that the rudiments of the inner part of the male genitalia of *Blatta* and *Periplaneta* are clearly present as a pair of outgrowths in the first and second nymphal instars and not as three outgrowths of phallomeres as described by Snodgrass (fig. 9, D & E, *pnv*). With regard to the observations of Snodgrass (1937) on the development of the male genitalia of *Blatta* and *Periplaneta*, it may be pointed out that his conclusions appear to be based on the dissections of well-grown nymphs, the earliest of those which he figures is 11 mm. long, and, according to my observations on the life history of *Blatta*, corresponds to the third nymphal instar. The sections of the first and second and the dissections of second nymphal instars of *Blatta* and *Periplaneta* clearly show that the early rudiments of the inner part of the male genitalia consist of only one pair of lobes already described as left and right penis valves. In the third instar, which is probably figured by Snodgrass as showing the earliest condition, each penis valve divides into a dorsal and a ventral part and since the left ventral penis valve is not well defined at this stage (pl. 4, fig. 30, *lvpnv*), and is incompletely separated from the right dorsal valve, it appears that Snodgrass has probably overlooked its morphological identity. In the adult, as noted above, all the four parts of the originally single pair of penis valves surround the male genital aperture which is situated between their bases.

The genital ducts : In the pronymphal instar of *Blatta*, as well as in the first instar nymphs of *Blatta* and *Periplaneta*, the *vasa deferentia* can be traced to the posterior end of the ninth segment, where each terminates into a hollow and closed sac, the " terminal ampulla." The *vasa deferentia* are solid strands at this stage. Each ampulla rests on the penis valve of its side and lies against the anterior end of the invagination of the median ejaculatory duct (pl. 4, fig. 31). It can be clearly observed that there is no connection with the ampullae and the median ejaculatory duct at this stage nor during the next nymphal stages of *Blatta* and *Periplaneta*.

In the succeeding instars the ampullae increase in size and the ejaculatory duct grows anteriorly to lie between them. During the final moult the walls of the ampullae give out buds which develop into the male accessory glands. Meanwhile the two ampullae which lie close together at the anterior end of the ejaculatory duct acquire a communication with the latter.

The conglobate gland arises separately from the ejaculatory duct as an ectodermal invagination between the dorsal and ventral parts of the left penis valves.

2. Tettigoniidae.

The study of the post-embryonic development of *Leptophyes punctatissima* (Bosc) forms the basis of the following observations on the development of the genitalia and genital ducts of the long-horned grasshoppers.

The female.

Adult organs : The female reproductive organs of various Tettigoniidae have been described by Fenard, Snodgrass (1903) and more recently by Cappe-de-Baillon (1919), and need but brief mention. In *Leptophyes* the ovaries lie on either side of the alimentary canal in the body cavity. The paired oviducts

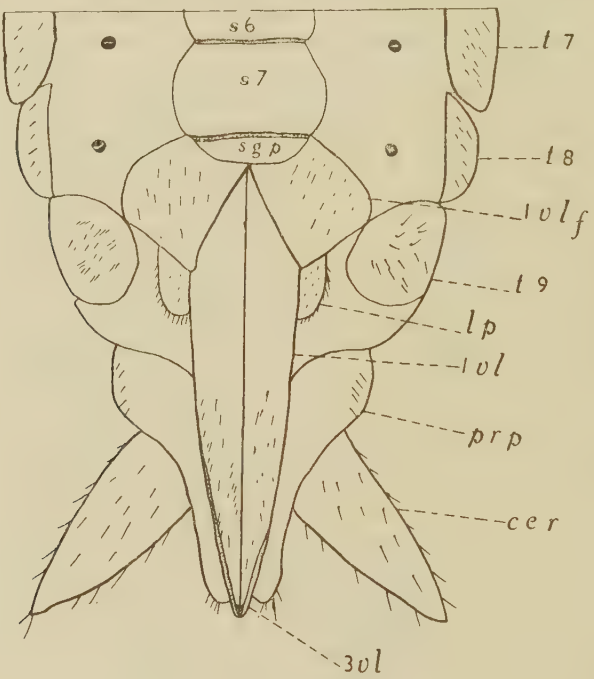

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Fig. 10.—Female genitalia of a full-grown nymph of *Leptophyes punctatissima*. *cer*, cercus; *lp*, lateral piece; *prp*, paraprocts; *vl*, ovipositor valve; *vlf*, valvifer.

unite together in the seventh segment below the alimentary canal, and the common oviduct thus formed opens on a subgenital plate of disputed nature. The genital cavity is formed between the combined bases of the anterior ovipositor valves and the subgenital plate referred to above. The spermatheca opens on the dorsal wall of the genital cavity behind the opening of the common oviduct, and further posteriorly, between the bases of the posterior valves, opens a single unbranched accessory gland.

The ovipositor of *Leptophyes*, like that of other Tettigoniidae, consists of fully developed anterior, posterior and lateral pair of valves and is highly compressed laterally (fig. 10). The subgenital plate, which lies below the base of the ovipositor, has been regarded as the reduced eighth sternum by Walker, Ford and Snodgrass, while Chopard, on the basis of his studies on the develop-

ment of *Pholidoptera femorata* (Fieber), regards it as an intersegmental outgrowth between the seventh and eighth sterna. Becker, on the other hand, in *Tylopsis liliifolia* (Fabr.) considers it to be formed by the fusion of the appendages of the seventh abdominal segment.

Development.

The genitalia : In the youngest nymph collected measuring 8 mm. in length, all the three pairs of the valves have been formed. The ninth sternum carries the lateral and posterior valves, while the anterior valves are borne by the eighth sternum.

During the further process of development the eighth sternum becomes membranous in the middle and a fold growing from the intersegmental region between the seventh and eighth sterna overtakes it from below. Gradually the whole of the eighth sternum becomes membranous except the lateral parts which form the bases of the anterior valves or the first pair of valvifers (fig. 10, *ivlf*). It is, therefore, evident that the subgenital plate is not formed by the eighth sternum. Each of the lateral parts of the eighth sternum have been termed pileolus by Chopard, first valvifer by Snodgrass and basivalvula by Walker, and represents the coxites of the eighth segment.

The genital ducts : In young nymphs the paired oviducts terminate on the hind margin of the seventh sternum in the form of a pair of ampullae lying on either side of the median ectodermal invagination which is the rudiment of the common oviduct. At this stage the nymphs of *Leptophyes* possess three median ectodermal invaginations in the hind region of the abdomen. The one behind the seventh sternum, as already stated, gives rise to the common oviduct and the others behind the eighth and ninth sterna form the spermatheca and the female accessory gland respectively.

The common oviduct divides at its anterior end into two short branches, each lying on one of the ampullae of the paired oviducts. These ampullae become enlarged and lie ventro-lateral to the anterior branches of the common oviduct. The posterior extension of the median oviduct corresponds to what has been described in BLATTIDAE : viz., by the formation and dorsal closure of an ectodermal groove along the mid-dorsal line of the subgenital plate (pl. 5, fig. 32).

The invagination behind the eighth sternum, as mentioned above, forms the spermatheca which grows anteriorly in the form of a tube after the manner described in *Blatta* (pl. 7, fig. 48, *spr*). The last invagination belonging to the ninth segment forms the accessory gland, which, unlike that of BLATTIDAE, is unbranched.

In the older nymphs the anterior short branches of the common oviduct communicate with the ampullae by the breaking down of the intervening walls (pl. 5, fig. 33), and the rest of the efferent system models itself after the fashion of the adult.

The male.

Adult organs : The male organs of TETTIGONIIDAE have been recently described by Snodgrass (1937) in a number of forms. In *Leptophyes* they resemble the male organ of *Orchelimum minor* Brunner described and figured by the same author. The testes of *Leptophyes* are a pair of large bodies lying on either side of the alimentary canal in the third and fourth abdominal segments. The *vasa deferentia* which emerge from the posterior end of the testes are highly

convoluted and open into the anterior end of the median ejaculatory duct along with a large number of accessory glands (fig. 11, A). The accessory glands consist of two sets. The first is composed of smaller tubes which are grouped medially behind the second set of larger glands which fill most of the posterior region of the body cavity. A pair of sac-like glandular pouches open on either side of the ejaculatory duct, and have been termed lateral glandular pouches by Walker, and vesicles of the ejaculatory duct by Snodgrass.

The male subgenital plate, like that of the other Orthoptera, is formed by the modified ninth coxo-sternum. It bends upwards posteriorly and is more or less truncated at its hind margin. Unlike *Blatta* and *Periplaneta*, there are no styli on the ninth sternum of *Leptophyes*. Well-developed styli are, however, present in a number of TETTIGONIIDAE, especially in *Meconema* and other allied forms, as shown by Chopard, and in some cases they are movably articulated with the ninth sternum.

The copulatory organ of *Leptophyes* is weakly sclerotised and consists of a pair of medially united dorsal and a pair of likewise medially united ventral valves. A thinly sclerotised plate lying over the base of the united dorsal valves may be regarded as a reduced pseudosternum which attains its greatest development in GRYLLIDAE described later.

Development.

The genitalia : In the youngest nymph collected, measuring about 5 mm. in length, the ninth sternum is bilobed posteriorly. These posterior lobes are much thicker than the sternum proper and appear to represent the appendages of the ninth segment in the process of fusion with the corresponding sternum. A similar process has been observed by Else in *Melanoplus differentialis* (ACRIDIDAE). The styli of the ninth sternum are wanting. The male genital cavity is formed between the free hind margin of the ninth sternum and the bases of the paraprocts in a manner similar to that of BLATTIDAE. Attached to the bases of the genital cavity there is a pair of penis valves, which in their shape and position resemble the paired penis valves of the young nymphs of *Blatta* and *Periplaneta* (fig. 11, B).

Following the next moult, each penis valve divides by a horizontal fissure appearing at its inner side, into a dorsal and ventral part (pl. 5, figs. 34 & 35). During the subsequent stages the penis valves grow in size, the dorsal part of each penis valve being larger than the ventral. Meanwhile the right and left dorsal and the corresponding ventral penis valves of either side approach each other and begin to fuse in the middle line. The ninth sternum at the same time becomes modified to form the subgenital plate or the hypandrium of the adult already described.

The above observations are contrary to the findings of Snodgrass (1937). He describes the origin of the inner part of the male genitalia of the TETTIGONIIDAE from several rudiments of which there are six in *Conocephalus fasciatus*. These rudiments have been designated phallomeres, two of which are regarded as dorsal, two ventral and two lateral. The development of *Leptophyes* clearly shows that there are only two penis valves in very young nymphs which are comparable with those of the first instar nymphs of *Blatta* and *Periplaneta*. Snodgrass, in this case also, appears probably to have drawn his conclusions from the study of the nymphs which seem to be fairly well grown and appear to have undergone a secondary modification. The youngest nymph of *Conocephalus* which he has figured measures 9 mm. in length and it is probable that the three pairs of phallomeres of such a well-grown

nymph might have resulted by the division of a single pair, which in *Leptophyes* also divides to give rise to two pairs of penis valves as described above.

The genital ducts : In the youngest nymph studied, a median invagination between the bases of the penis valve marks the origin of the ejaculatory duct. Lying on either side of the anterior end of the ejaculatory duct and resting on the basis of the penis valves there is a pair of ampullae corresponding to those of *Blatta*. The ampullae of *Leptophyes* are, however, very large and constricted in the middle. The *vasa deferentia* (*vd*) communicate with the ampullae from the posterior side and are solid during the early nymphal stages (pl. 5, fig. 36).

In the older nymphs a groove across round the middle of each ampulla and divides it into an anterior and posterior part (pl. 5, fig. 37). This division of the ampullae appears to be a characteristic feature of *Leptophyes* and seems

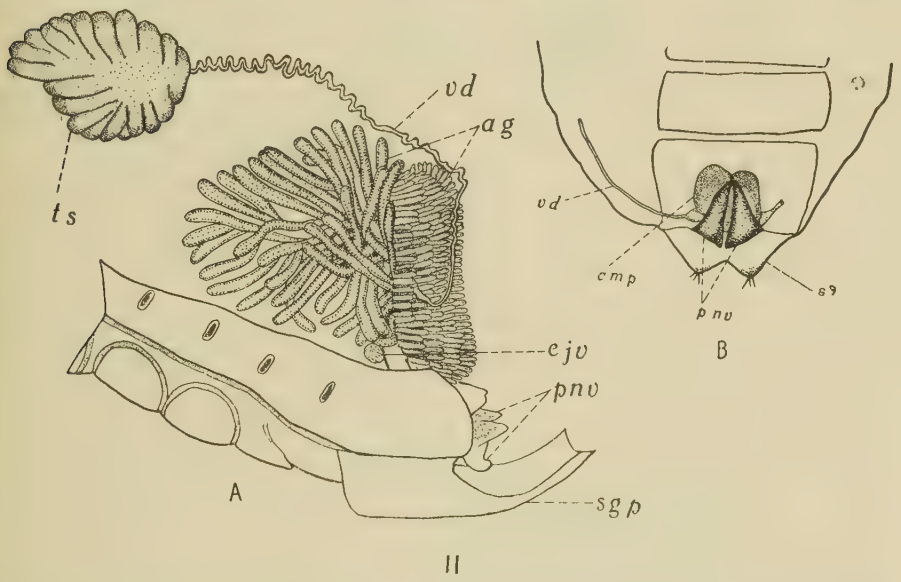

Fig. 11.—*Leptophyes punctatissima*—A, male reproductive organs of adult. B, male genitalia of a young nymph, 6·5 mm. long. *ag*, accessory glands; *amp*, ampullae; *ejv*, ejaculatory vesicle; *pnv*, penis valves; *sgp*, subgenital plate; *ts*, testis; *vd*, vas deferens.

to be related with the development of two kinds of male accessory glands. The latter make their appearance towards the final moult and arise from the walls of the ampullae in a manner similar to that described in Blattidae. During the final moult, the *vasa deferentia* become highly convoluted, and the vesicles of the ejaculatory duct arise from the wall of the latter.

3. Gryllidae.

The post-embryonic development of the genitalia and the genital ducts was studied in the common European house-cricket *Gryllulus domesticus* (L.) and in *Gymnogryllus erythrocephalus* (Serv.), a North-Indian cricket. The fundamental facts of the development are more or less identical in both the above-mentioned forms, hence the following account dealing with *G. domesticus* is equally applicable to *G. erythrocephalus*.

The female.

Adult organs : The female reproductive organs of *G. assimilis* have been recently described by Snodgrass (1933) and by Spann (1934) and those of *G. domesticus* by Cappe-de-Baillon (1919). The ovaries lie dorso-lateral to the alimentary canal. Each ovary consists of a number of closely packed ovarian tubes which open into the paired oviducts. The latter gradually descend to the floor of the abdominal cavity in the seventh segment and unite below the alimentary canal to form the common oviduct which opens at the base of the

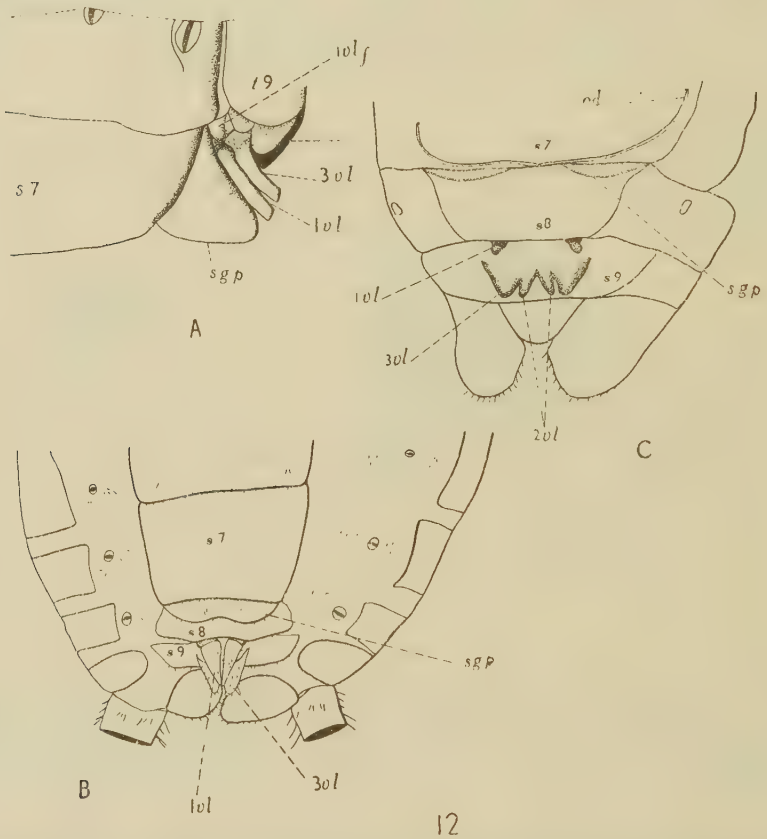

Fig. 12.—*Gryllulus domesticus*—A, female genitalia, lateral view. B, ventral view of the abdomen of a third instar female nymph. C, internal view of the genitalia of second instar female nymph. *od*, oviduct; *sgp*, subgenital plate; *vl*, ovipositor valves; *vlf*, valvifer.

subgenital plate on the ventral surface of the female genital cavity. The spermatheca opens on the dorsal wall of the latter by a median aperture which is located between the bases of the ventral ovipositor valves. It consists of a terminal spermathecal sac, which is followed by a narrow and convoluted duct opening into the genital cavity through a wide sac or pouch.

The female genitalia of adult *G. assimilis* has been described by Walker (1919), Snodgrass (1933) and more recently by Spann (1934). In *G. domesticus* the main features of the genitalia are in agreement with those of *G. assimilis*

(fig. 12, A). The small subgenital plate of GRYLLIDAE has been referred to as the eighth sternum by Walker, Ford and Snodgrass, while Chopard on the basis of his studies on the development of *Gryllomorpha dalmatina* regards it as an intersegmental outgrowth between the seventh and eighth sterna. Becker regards the subgenital plate of *Oecanthus pellucens*, like that of TETTIGONIIDAE, to have been formed by the fusion of the appendages of the seventh abdominal segment. The ovipositor of *G. domesticus* consists of three pairs of valves, the anterior, posterior and lateral. The posterior valves are extremely reduced and have often been overlooked.

Development.

The genitalia : In the first instar nymphs the sexes cannot be distinguished, since the rudiments of the genitalia are not visible from the outside. Transverse sections passing through the hind margin of the eighth and ninth sterna, however, reveal the presence of the rudiments of the anterior and lateral valves.

In the next instar the female genitalia are fairly prominent. On the hind margin of the ninth sternum the lateral valves can be easily observed. The posterior valves are also present on the inner margin of the latter and appear to be median outgrowths (fig. 12, B).

The eighth sternum of *Gryllulus* and *Gymnogryllus* does not divide into two lobes by a median cleft in the first and second instars. This feature is probably peculiar to GRYLLIDAE. In the second instar a pair of palp-like outgrowths appears on the hind margin of the eighth sternum. These are the forerunners of the anterior valves. The early rudiments of the anterior valves develop in GRYLLIDAE far apart from the middle line and in no way can they be regarded as medial outgrowths of the coxites of the eighth segment or homologous with the posterior valves of the ninth segment (pl. 6, fig. 39).

Meanwhile a pair of folds appears on either side of the hind margin of the seventh sternum (fig. 12, C, *sgp*). These folds grow quickly and unite to form a single plate which lies below the eighth sternum covering its base (fig. 12, B). Becker regards the rudiments of the subgenital plate of GRYLLIDAE as the appendages of the seventh segment, which according to him fuse to form the subgenital plate of the adult. It may be pointed out that these early folds of the hind margin of the seventh sternum are simply intersegmental outgrowths (pl. 6, fig. 40), and have nothing to do with the seventh pair of embryonic abdominal appendages which are lost long before the appearance of the above folds.

During the next instars the changes which occur in the region of the genitalia are of great magnitude. They mask the true mode of origin of a number of structures involved. In the ninth segment the lateral and posterior valves grow in size and absorb the median part of the ninth sternum lying between their bases. On either side of the lateral valves a small part of the antero-lateral region of the ninth sternum escapes the fate of being absorbed by the growing ovipositor valves of that segment and persists until the final moult when it is fused with the posterior margin of the first pair of valvifers.

In the same instar, a median invagination appears on the hind margin of the eighth sternum and divides the posterior part of the latter into two lobes, as seen in the cockroach. With the appearance of this invagination the anterior valves, which were formerly far away from each other, are dragged towards the middle line and lie below the posterior valves (fig. 12, B).

The subgenital plate, which in the preceding instar was confined to the base of the eighth sternum, now grows posteriorly to cover the whole of the latter,

with the result that the eighth sternum becomes almost membranous except for the posterior parts which form the first pair of valvifers. The anterior valves articulate with these valvifers by means of distinct joints. The eighth sternum, in this way, is replaced by the new subgenital plate which, as shown above, is an outgrowth from the intersegmental region between the seventh and eighth sterna. These observations are in agreement with those of Chopard on the development of *Gryllomorpha* and are opposed to the views held by Walker, Ford and Snodgrass. Walker states that the subgenital plate of *Gryllulus* is formed by the infolding of the eighth sternum itself, so that a part of it forms the former plate and the rest of it is included in the inner lining of the genital cavity. This statement does not receive any support from the development of *Gryllulus* and *Gymnogryllus* in which the subgenital plate appears as a new structure from the intersegmental region between the seventh and eighth sterna without any trace of the infolding of the eighth sternum.

The other argument is based on the studies of musculature, particularly those of Ford (1923) (*vide* Walker and Snodgrass). These studies chiefly deal with the musculature of the adult insects. The changes that take place during the final moult, specially in the region of genitalia, are of a very complicated nature, so that a number of sclerites shift their position while others fuse with different sclerites to form structures of composite nature. In view of these complicated changes, the musculature of the adult cannot override the evidence derived from development. Apart from that, the differences in the musculature of the eighth sternum among various families of Orthoptera are also very great, and have not been accounted for. According to Ford herself, in *Melanoplus bivitatus* (Acrididae) the musculature of the eighth sternum is almost typical, while it is totally wanting in the subgenital plate of *Gryllus* [*Gryllulus*] *assimilis* (Gryllidae). The above differences have not been accounted for by Ford, and may be held to indicate the different nature of the subgenital plates of Acrididae and Gryllidae.

The subsequent development consists chiefly of the growth of the structures already mentioned. The posterior valves do not develop but remain rudimentary, and are concealed between the bases of the highly developed lateral valves. The anterior valves are fully developed and form the ventral elements of the ovipositor shaft. The posterior parts of the eighth sternum, which support their bases, fuse with the antero-lateral parts of the ninth sternum to form the first pair of valvifers, which also according to Chopard and Snodgrass are composite structures in Gryllidae, formed after the manner described above (fig. 12, A, 1*vlf*).

The genital ducts: In the first and second instars the oviducts can be traced to the posterior margin of the middle line (fig. 12, C, *od*). During these stages there are no traces of the ectodermal invaginations in the seventh or in the following abdominal segments. In the third instar a rudimentary invagination, which corresponds to the invagination of the accessory glands in Blattidae, appears on the hind margin of the ninth sternum between the bases of the inner valves. The spermathecal invagination, as stated above, does not appear until the late third stage. In the full-grown third instar nymphs, the above-mentioned invagination grows anteriorly in the form of a tube which ultimately forms the spermatheca (pl. 6, fig. 41). In the same instar an ectodermal thickening at the base of the subgenital plate marks the rudiment of the common oviduct (*cod*). The ampullae of the paired oviducts lie on either side of the median oviduct.

During the further development, the spermatheca grows anteriorly and

becomes a coiled tubular organ. The common oviduct grows for a short distance on the dorsal surface of the subgenital plate by the formation of an ectodermal groove which closes on its dorsal surface. The common oviduct opens on the ventral surface of the genital cavity as in the case of BLATTIDAE and TETTIGONIIDAE.

The male.

Adult organs: The male reproductive organs of GRYLLIDAE have been described by Fenard (1896) and Schimmer (1909) among the earlier workers. Quite recently the male organs of *Gryllus* [*Gryllulus*] *assimilis* have been figured and described by Spann (1934) and Snodgrass (1937). The testes of *G. domesticus* lie from the third to the sixth abdominal segments dorso-lateral to the alimentary canal (fig. 13, A). Each testis consists of a number of closely aggregated follicles forming a disc-shaped body. The *vasa deferentia* are narrow and run towards the posterior end on either side of the alimentary canal. At its hind end each *vas deferens* takes a turn towards the front and enters into the bunches of the accessory glands to open into the anterior end of the ejaculatory duct. The terminal parts of the *vasa deferentia* are swollen and according to Spann form the seminal vesicles of the adult.

The male accessory glands consist of a number of slender tubes which are closely aggregated together. The more median and dorsal tubes are slightly smaller than the ventral and peripheral tubes. A pair of small glandular sacs (*ejv*) corresponding to those of *Leptophyes* (TETTIGONIIDAE) is also present in *Gryllulus*, which opens on either side of the ejaculatory duct.

The male genitalia of *G. assimilis*, along with that of a number of other Gryllids, have been fully described by Chopard, Walker and Snodgrass. The male genitalia of *G. domesticus* closely resembles that of *G. assimilis* (fig. 13, B). The subgenital plate or the hypandrium is formed by the enlarged trough-shaped ninth sternum which does not carry styli as found in BLATTIDAE. The copulatory organ which is enclosed within the subgenital plate is roofed by a well-developed sclerite termed variously "pseudosternum," "pseudepiphalle" or the "anchre" (*pst*). Below it there is a pair of sclerites which Walker terms ectoparameres (*ecpm*). The male gonopore is bounded ventrally by a pair of membranous lobes, the ventral penis valves. A special feature of the male genitalia of GRYLLIDAE is the presence of a large sac opening dorsal to the aperture of the ejaculatory duct (*spp*). This sac has been termed spermatophore sac by Walker and dorsal cavity by Snodgrass. On the sides of the spermatophore sac there is a pair of sclerites which Walker terms endoparameres (*enpm*). Another pair of sclerites, the rami (*rm*), run downward and backward from the pseudosternite to lie on either side of the base of the male organ.

Development.

The genitalia: In the first instar nymphs the rudiments of a pair of penis valves corresponding to those of BLATTIDAE and TETTIGONIIDAE can be easily observed attached to the base of the genital cavity formed between the ninth and tenth sterna (pl. 6, fig. 42). The form, as well as the position of paired penis valves of *Gryllulus* (fig. 13, D), and *Gymnogryllus* are similar to what has been described in *Periplaneta*, *Blatta* and *Leptophyes*.

During the following stages the penis valves grow in size and tend to unite at their dorsal surface. In well-grown nymphs the penis valves can be seen as pointed structures and are divided into dorsal and ventral parts correspon-

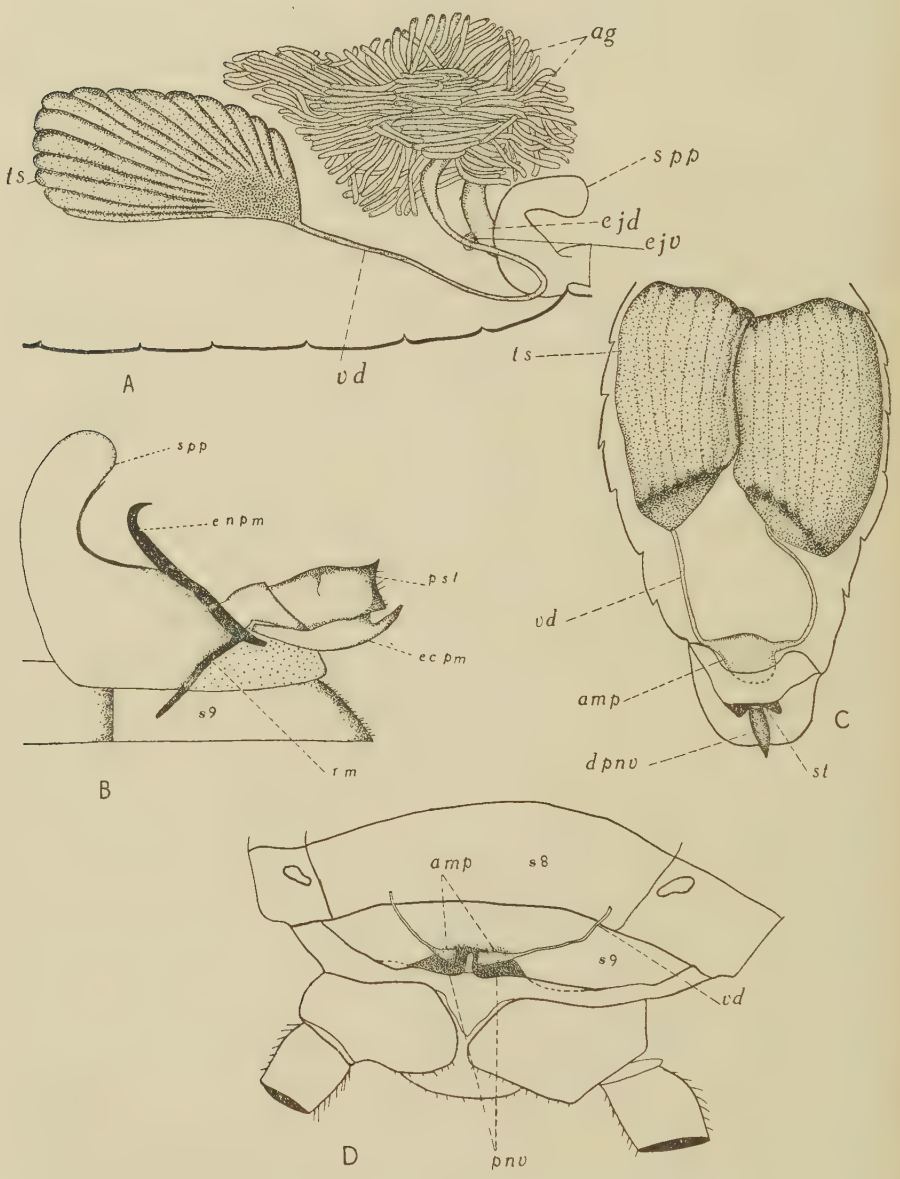

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FIG. 13.—*Gryllulus domesticus*—A, male reproductive organs. B, male genitalia. C, same in a fifth instar nymph. D, same in a second instar nymph. *ag*, accessory glands; *amp*, ampullae; *ecpm*, ectoparamere; *ejd*, ejaculatory duct; *ejv*, ejaculatory vesicle; *enpm*, endoparamere; *pnv*, penis valves; *pst*, pseudosternum; *rm*, rami; *spp*, spermatophore sac; *ts*, testes; *vd*, vasa deferentia.

ding with the division of the penis valves of Blattidae and Tettigoniidae. In *Gryllulus* the dorsal valves are much larger than the ventral valves and for the most part are united in the mid-dorsal line. This modification appears to have resulted probably by the formation of the spermatophore sac. The ventral penis valves are membranous and rudimentary, and lie below the male gonopore.

During the final moult the united dorsal penis valves invaginate to form the spermatophore sac. The rudiment of the pseudosternite can be observed in the older nymphs as a transverse cuticular strip at the bases of the united dorsal valves (fig. 13, C, *pst*).

The changes during the final moult are extremely rapid and drastic. The median part of the united dorsal penis valves invaginates to form the spermatophore sac, and a number of sclerites referred to above as ectoparameres, endoparameres and rami are probably derived from the various parts of the dorsal penis valves. The pseudosternum becomes highly sclerotised and forms an arch over the male organ of the adult.

The genital ducts : In the first instar nymphs the *vasa deferentia* can be traced to the posterior end of the ninth sternum, where they terminate into hollow ampullae (pl. 6, fig. 43). Each terminal ampullae rests on the penis valve of its side (fig. 13, D). The rudiment of the median ejaculatory duct is also present at this stage in the form of a median invagination between the bases of the penis valves, and the ampullae lie on either side of the anterior end of it. The efferent system of the early nymphal instars of *Gryllulus* is comparable with the corresponding stages of Blattidae and Tettigoniidae.

In the succeeding instars an asymmetry marks a characteristic feature of Gryllidae (pl. 6, fig. 44). The left ampullae becomes larger than the right, and the two closely approximated ampullae along with the anterior end of the ejaculatory duct bend backward and upward forming a loop (pl. 6, fig. 44). In the last instar the accessory glands make their appearance in the form of a number of buds on the walls of the ampullae which ultimately open conjointly into the anterior end of the ejaculatory duct. The spermatophore sac of *Gryllulus*, as stated above, is formed by the invagination of the median part of the united dorsal penis valves during the final moult and open dorsal to the aperture of the ejaculatory duct.

4. Acrididae.

The study of the postembryonic development of *Locusta migratoria migratorioides* R. & F., *Schistocerca gregaria* (Forsk.) and *Poecilocercus pictus* (Fab.) forms the basis of the following observations on the development of the genitalia and efferent genital ducts of Acrididae. The main features of the development and morphology of the adult organs, except for some minor details especially in the adult male genitalia, are almost in agreement in all three forms. In the following description *L. migratoria migratorioides* serves as the type, but the main conclusions are equally applicable to *S. gregaria* and *P. pictus*.

The female.

Adult organs : The female organs of Acrididae are well known. Among the recent workers Harman (1925), Fedorov (1927) and Snodgrass (1935) have described the adult organs of various Acrididae. The female organs of *L. migratoria* have been described and figured by Sokolow (Uvarov, 1928). In *L. migratoria migratorioides* the ovaries are united with each other along the

middle line, dorsal to the alimentary canal. Each lateral oviduct is produced anteriorly in the form of an accessory gland which is supposed to secrete an albuminoid substance. Posteriorly the paired oviducts unite below the alimentary canal to form the median oviduct which opens on the ventral surface of the genital cavity formed between the combined bases of the anterior valves and the free hind margin of the eighth sternum (fig. 14). A little behind the opening of the common oviduct there is a median opening of a blind pouch of unknown function. The spermatheca (*spr*), which consists of a highly convoluted tube and a terminal sac, opens on the common oviduct.

The external genitalia of the female Acrididae have been described by a number of workers, the comparative studies of Walker (1919), Chopard (1920) and of Snodgrass (1931–35) needing special mention. The subgenital plate of

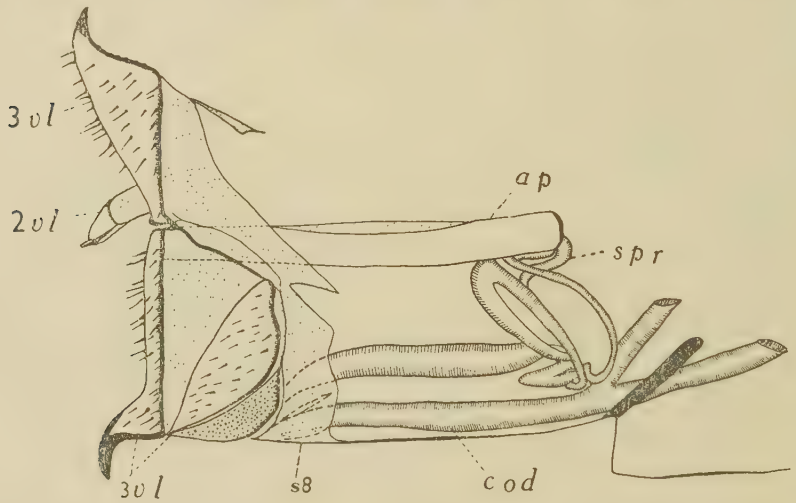

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Fig. 14.—Female genitalia of *Locusta migratoria*. *ap*, apophysis; *cod*, common oviduct; *spr*, spermatheca; *vl*, ovipositor valves.

Acrididae is formed by the eighth sternum, which on its hind margin bears a median process—" the egg guide "—a characteristic feature of Acrididae. The ovipositor of all the forms studied consists of three pairs of valves of which the posterior or inner valves are comparatively reduced (*2vl*). Two long sclerotised bars (*ap*), which articulate at their posterior and run dorso-laterally in the body cavity, have been termed by Walker " the process of intersegmental apophyses." These processes also form a characteristic feature of the female genitalia of Acrididae.

Development.

The genitalia : In the pronymphal and in the first instar the sexes can be distinguished by examining the ninth sternum. In the female it is deeply bilobed at its hind margin (fig. 16, A). These two posterior lobes are the forerunners of the lateral valves. No posterior or inner valves are present at this stage. The hind margin of the eighth sternum in the same instar is also bilobed owing to the presence of a median spermathecal invagination. These posterior

lobes of the eighth sternum mark the rudiment of the first pair of valvifers or the gonocoxites of the eighth segment which form the bases of the anterior valves.

During the second stadium the lateral valves become more deeply separated and the posterior valves make their appearance as medial outgrowths of their bases. Each coxite of the eighth sternum referred to above is divided by a vertical groove into an inner and a lateral part during the same instar (pl. 7, fig. 45). The inner subdivision forms the anterior valves, while the outer one forms their basal plates or the first pair of valvifers, also known as basivalvulae.

It may be pointed out that Nel in *Locustana* and *Colemania* homologises the anterior valves with the lateral valves. His sections of the first instar nymphs of the above-mentioned forms agree with those of the forms I have studied (pl. 7, figs. 46 & 47). It appears that Nel, as in BLATTIDAE, regarded the coxites of the eighth sternum as the anterior valves. The anterior valves of ACRIDIDAE do not develop till the second instar, when a marked groove clearly defines them from the coxites of the eighth sternum or the first pair of valvifers (pl. 7, fig. 46).

In the following instars the development of ACRIDIDAE offers a feature distinct from the other Orthoptera already described. The first pair of valvifers with the anterior valves are separated from the eighth sternum and approach each other. The eighth sternum does not become membranous like that of BLATTIDAE, TETTIGONIIDAE and GRYLLIDAE but grows posteriorly below the bases of the anterior valves, to form the subgenital plate of the adult. Meanwhile the lateral valves grow enormously in size and most of the ninth sternum is absorbed by their growing bases. The posterior valves are comparatively less developed.

The intersegmental apophysis, which has been mentioned as a structure of doubtful nature by Walker, arises during the final moult from the region between the bases of the lateral and anterior valves, and, therefore, represents an intersegmental apodeme.

The genital ducts : In the newly hatched *Locusta* the paired oviducts can be traced to the hind margin of the seventh sternum, where they end into ampullae corresponding to those described by Nel and Roonwal. Three median ectodermal invaginations are present at this stage in the hind abdominal region. The anterior one which marks the rudiment of the common oviduct lies behind the seventh sternum in the intersegmental region (pl. 7, fig. 48, *codin*). The next behind the eighth represents the rudiment of the spermatheca and the last which is found on the hind margin of the ninth sternum corresponds to the accessory gland invagination of BLATTIDAE and TETTIGONIIDAE (again).

Roonwal locates the origin of the common oviducal invagination of *Locusta* on the anterior margin of the eighth sternum. An examination of the figures (pl. 7, figs. 48 & 49), however, shows that the area which represents the original place of the invagination does not belong to the eighth sternum at all, but represents that of the reduced intersegmental outgrowth (*ep*) or the "epigynum," and at this stage represents the position of the gonopore of BLATTIDAE, TETTIGONIIDAE and GRYLLIDAE.

During the following stages the common oviduct extends from the hind margin of the seventh sternum to the hind margin of the eighth by the ventral closure of an ectodermal groove stretching along the middle line of the eighth sternum in a similar manner to *Locustana* and *Colemania* as described by Nel.

The ectodermal invagination behind the eighth sternum forms the spermatheca in the same way as in other Orthoptera, while the invagination of the

hind margin of the ninth sternum, like the corresponding invagination of the Gryllids, remains undeveloped.

The male.

Adult organs : The male organs of ACRIDIDAE, like the female organs, are fairly well known (*vide* Fenard, Harman, Fedorov, Snodgrass and others). The adult organs of *Locusta migratoria* have been described by Iwanova (Uvarov, 1928). The compound testis (fig. 15, A) of *Locusta migratoria migratorioides* lies in the fourth and fifth abdominal segments dorsal to the alimentary canal. The two *vasa deferentia* running posteriorly encircle the alimentary canal and open into the anterior end of the median ejaculatory duct. The accessory glands consist of a number of blind tubes which also open into the anterior end of the ejaculatory duct. A pair of these accessory gland tubes, which is orange-yellow in colour like the testis, serves to store the spermatozoa. Similar tubes serving as seminal vesicles have also been reported by Fedorov and Ito in other ACRIDIDAE. The median ejaculatory duct runs along the venter of the ninth abdominal segment where it enters into the intromittent organ. Prior to its entrance into the copulatory organ, the ejaculatory duct is swollen and is strongly musculated, forming what has been termed the ejaculatory sac by Snodgrass (fig. 15, B, *ejs*).

The male genitalia of ACRIDIDAE are highly developed and characteristic. The various parts have been often described with different terminology by different workers. In the present description Walker's terminology will be employed, since it is simpler and more widely known. The ninth sternum, like that of other Orthoptera, is modified to form the subgenital plate. It is highly developed and trough-shaped with its posterior margin rounded and bent upward. The copulatory organ is ensheathed in a membranous envelope and consists of a pair of dorsal and ventral penis valves which together form the main intromittent organ or " aedeagus " (fig. 15, B). The ventral valves are united for the most of the part along the mid-ventral line. The dorsal valves are also fused together proximally and form a meatus-like structure.

Dorsal to the intromittent organ there is a transverse sclerotised bar of which the ends are produced anteriorly to form a pair of sclerotised bars called the endapophyses (*enap*). The base of the aedeagus is heavily sclerotised and is produced towards the anterior end in the form of wing-like processes (*enpm*) termed endoparameres by Walker. The pseudosternum or epiphallus (*pst*) consists of a series of sclerites which are attached to the membrane overhanging the base of the copulatory organ. The male genitalia of *Schistocerca gregaria* and *Poecilocercus pictus* differ in a number of details from that of *Locusta migratoria* but the fundamental plan is the same in all of them.

Development.

The genitalia : In the first instar of *L. migratoria* and others the ninth sternum is bilobed posteriorly and a faint suture runs transversely below the bases of the above-mentioned posterior lobes of the ninth sternum (fig. 15, C). According to Else, this suture represents the point of the fusion of embryonic appendages of the ninth segment with the ninth sternum. The genital cavity is bounded ventrally by the free hind margin of the ninth sternum, while the dorsal wall is formed by a membrane lying anterior to the base of the paraprocts and is regarded as the membranous tenth sternum by Else. At the base of the genital cavity there is a pair of ectodermal outgrowths—the penis valves —which in their form and position are identical with the penis valves of other

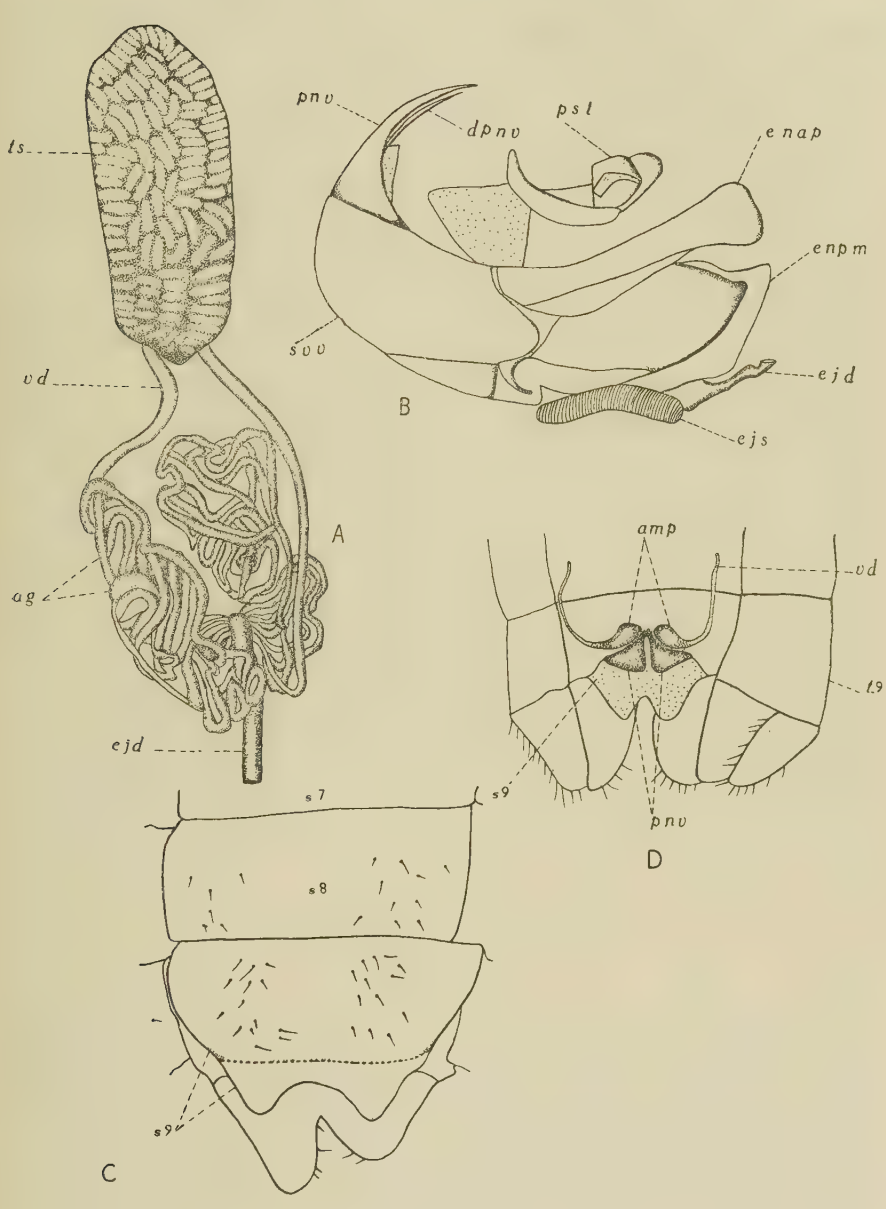

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FIG. 15.—*Locusta migratoria*—A, male reproductive organs. B, lateral view of male nymph. C, ventral view of the first instar male nymph. D, internal view of the male genitalia of first instar nymph. *ag*, accessory gland; *amp*, ampullae; *ejd*, ejaculatory duct; *ejs*, ejaculatory sac; *enap*, endapophysis; *enpm*, endoparamere; *pnv*, penis valve; *pst*, pseudosternum; *suv*, subventral valves; *ts*, testis; *vd*, vasa deferentia.

Orthoptera described previously (fig. 15, D). Else, in *Melanoplus differentialis*, also described a similar pair of penis valves and has traced them to the embryonic appendages of the tenth abdominal segment.

In the succeeding instars the penis valves grow much in size and each becomes differentiated into a narrow posterior part and a broad basal region. At the same time a pair of folds develops on the ventral surface of the bases of the penis valves on either side of the genital cavity and unites in the middle line below the penis (pl. 7, fig. 50, *svl*). This fold divides the genital cavity into dorsal and ventral compartments and forms in the adult a fold at the base of the intromittent organ, termed by Walker the subventral lobe.

The division of each penis valve into a dorsal and ventral part occurs at the end of the nymphal life and is restricted to the posterior apices of the penis valves. As a result of this horizontal cleft, they are divided into dorsal and ventral parts corresponding to those of the other Orthoptera. During the final moult the changes in the male genitalia are of a drastic nature, so that a number of different structures make their appearance. The transverse bar, the endapophyses and the endoparameres appear to arise from the broad bases of the penis valves, and the pseudosternum is developed as a group of sclerites in the membrane that arches over the base of the penis valves.

The genital ducts : In the newly hatched *Locusta* and others between the bases of the penis valves there is a median invagination which forms the ejaculatory duct. On either side of its anterior end and resting on the bases of the penis valves there is a pair of ampullae which are comparable with those of the other Orthoptera described previously (pl. 7, fig. 51, *amp*). These ampullae of *Locusta* and *Melanoplus* have been described as the remnants of the embryonic coelomic pouches of the tenth abdominal segment by Else and Roonwal. The *vasa deferentia* (*vd*) in the youngest nymphs can be traced as solid strands communicating with the ampullae in the manner found in other Orthoptera.

The accessory glands arise from the wall of the ampullae towards the end of nymphal life, but much earlier than in the other forms studied above, and together with the *vasa deferentia* open into the anterior end of the ejaculatory duct.

VI. General Conclusions.

A. The female.

The genitalia : The foregoing account of the development of the female genitalia shows the extent of variation and modification undergone by the Orthopteroid insects. In the Ephemeroptera no traces of an ovipositor appear during postembryonic development. In the Dermaptera many of the forms are without an ovipositor in the adult. In *Forficula auricularia* even its traces have been deleted from the ontogeny. In some apparently primitive forms belonging to Labiduroidea, Zacher and Crampton have described an ovipositor which is specially well developed in *Echinosoma* and *Kalocrania* and consists of two pairs of valves.

In Plecoptera the rudiments of the anterior valves appear during the early period of postembryonic development, but they remain undeveloped. The processes of the eighth sternum of some adult stoneflies like *Perla*, *Perlodes*, *Pteronarcys*, and others, have been regarded as true anterior valves by Walker. These are secondary structures and have nothing to do with the rudiments of the true anterior valves.

Among the Orthoptera *sensu stricto* an ovipositor is typically present and

consists of all the three pairs of valves. The homologies and nature of these valves require a special consideration.

The chief facts of the development of various valves are briefly summarised below. The lateral valves are developed as the modified coxites of the ninth segment which, in BLATTIDAE, carry styli until the final moult. The posterior, or median, valves are the medial outgrowths of the bases of the lateral valves and make their appearance during the postembryonic development in the second or third instars.

The development of the anterior valves occurs in a different way in different groups of Orthoptera. In BLATTIDAE and ACRIDIDAE the coxites of the eighth segment are already differentiated from the sternum in the first instar owing to the presence of a median invagination on the hind margin of the eighth segment. Towards the end of the second instar a vertical groove divides each of them into a median and a lateral part. The median parts outgrow the lateral and form the anterior valves. The lateral parts form their supporting bases and have been termed the first pair of valvifers by Snodgrass and basivalvulae by Walker and others.

In GRYLLIDAE the rudiments of the anterior valves are present in the first instar nymphs on the posterior margin of the eighth sternum far away from the middle line. During the next stage they make their appearance in the form of papillae near the postero-lateral angles of the eighth sternum. Unlike BLATTIDAE and ACRIDIDAE, the spermathecal invagination of GRYLLIDAE does not appear till the third stage, and this fact is responsible for the difference in the development of the anterior valves in these forms. In the succeeding instars, the anterior valves of *Gryllulus* and *Gymnogryllus* move towards the middle line, as a result of the appearance of the spermathecal invagination, and lie on either side of the middle line below the posterior valves. They are at this stage already differentiated into basal coxites or first pair of valvifers and distal shafts or the anterior valves which are articulated with the former by a distinct joint.

In *Leptophyes* (TETTIGONIIDAE) the anterior valves are already well developed in the youngest nymphs studied, but the figures and account of the development of *Tettigonia* (*Locusta*) *viridissima* given by Dewitz, and also Walker's figure 9 (1919, *Ann. ent. Soc. Amer.* **12**) showing the development of the ovipositor in a young nymph of *Conocephalus faciatus*, 4 mm. long, indicate that the anterior valves of TETTIGONIIDAE probably develop in the same manner as those of GRYLLIDAE.

The above facts of development of the anterior valves call for special consideration. The apparent difference in the development of the anterior valves of BLATTIDAE and ACRIDIDAE on the one hand, and those of GRYLLIDAE and TETTIGONIIDAE on the other, is difficult to interpret, but two conclusions may be drawn. First that the anterior valves are not homologous structures among various families of Orthoptera; and while in BLATTIDAE and ACRIDIDAE they represent the medial outgrowths of the coxites of the eighth segment corresponding to the gonapophyses of Thysanura, in GRYLLIDAE and TETTIGONIIDAE they appear as posterior or distal outgrowths of the coxites probably homologous with the styli of the eighth segment of *Machilis* and other Thysanura.

The second conclusion drawn from the development of all the forms taken together, is that the original mode of the development of the anterior valves is represented by the condition found in GRYLLIDAE, and by the appearance of the spermathecal invagination, they are secondarily dragged towards the middle

line. Since in Blattidae and Acrididae the median invagination behind the eighth sternum is present in the youngest nymphs, their rudiments might have moved towards the middle line from their original position, with the result that the anterior valves arise on either side of the middle line (figs. 16 & 17). If the second conclusion is accepted, the anterior valves may be regarded as homologous structures among all the families of Orthoptera. There remains then the question of their nature as well as that of their homology with the

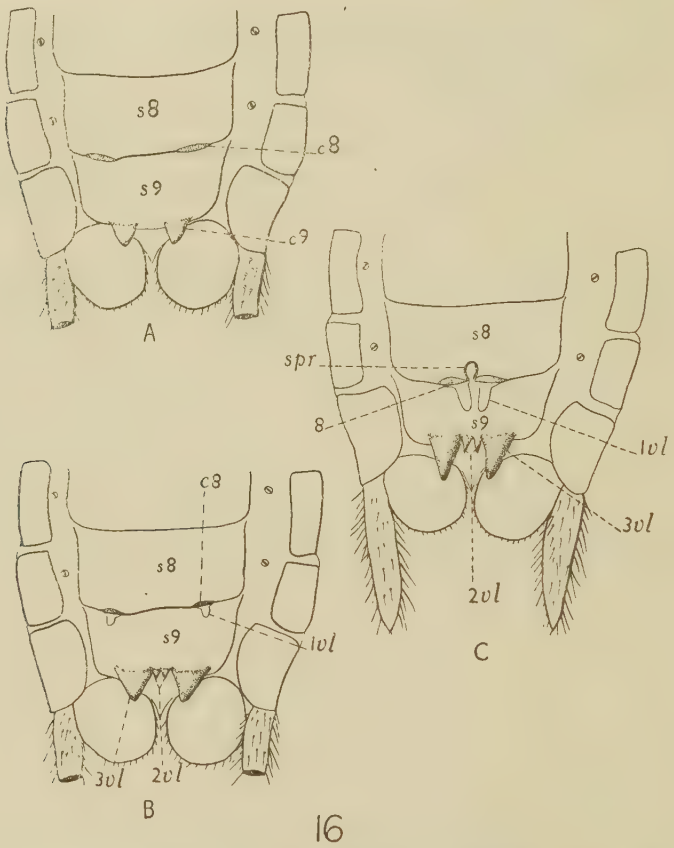

Fig. 16.—Diagrammatic figures of the development of ovipositor valves in a Gryllid. A, first instar. B, second instar. C, third instar. *c*, coxite; *spr*, spermatheca; *vl*, valves of the ovipositor.

other ovipositor valves. It may definitely be stated that the anterior valves of Gryllidae cannot be compared with the gonapophyses of the eighth segment of Thysanura. The second interpretation, that they represent the drawn-out or modified coxites of the eighth segment corresponding to the lateral valves, does not hold good, since the anterior valves become clearly differentiated from the coxites of the eighth segment by a distinct joint quite early during their development (fig. 12, B). Keeping these facts in view, they can only be homologised with the styli borne by the coxites of the eighth segment in Thysanura and I am inclined to adopt this view.

There are unfortunately not many complete accounts of the development of the ovipositor valves in the Exopterygota, and in many of the forms studied the spermathecal invagination is already present prior to the differentiation of the anterior valves from their bases (*vide* George, Nel, Metcalfe and others). George in the case of *Agrion* (Odonata), however, reports the presence of a pair of medial processes at the bases of the anterior valves and has failed to explain their nature. It is possible that these structures might correspond to the gonapophyses of the eighth segment of Thysanura, as also believed by Nel. Then the anterior valves of Odonata can only be compared with the styli of the eighth segment, since they are clearly differentiated from their bases, which according to George represent the coxites of the eighth segment. The total absence of the styli from the eighth sternum of all the known Pterygota, while those of the ninth segment are present in a number of forms belonging to Orthoptera, Isoptera and Odonata, also provides strong though indirect evidence in favour of the above-mentioned view.

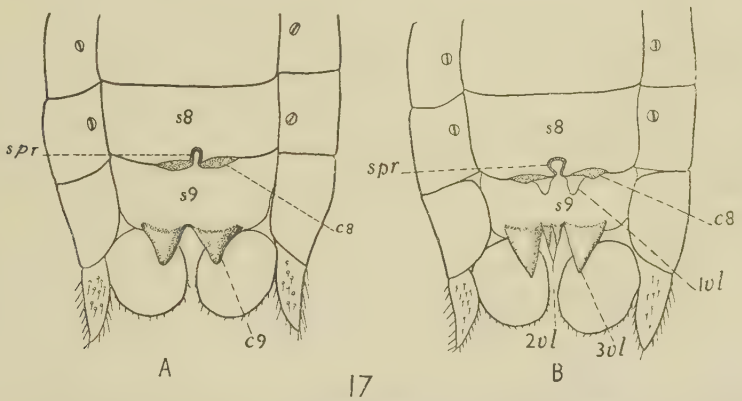

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Fig. 17.—Diagrammatic figures of the development of ovipositor valves in an Acridid and other Orthoptera. A, first instar. B, second instar. *c*, coxite. *spr*, spermatheca; *vl*, valves of the ovipositor.

In the face of the last-mentioned conclusion, the anterior valves of Orthoptera can be homologised neither with the posterior nor with the lateral valves, but can be regarded as homodynamous with the styli borne on the ninth sternum of the male and female Blattidae and other Orthoptera. The nature and homologies of the various valves of Orthoptera in the light of the above conclusions briefly stated are as follows :—

1. Lateral (dorsal) valves—drawn-out or modified coxites of the ninth segment.
2. Posterior (inner) valves—median outgrowths of the lateral valves corresponding to the gonapophyses of the ninth segment of Thysanura.
3. Anterior (ventral) valves—distal outgrowths (telopodites) of the coxites of the eighth segment, probably homologous with the styli on the coxites of the eighth segment of Thysanura.

Among the other Orthopteroid groups, in Isoptera an ovipositor is found in *Mastotermes darwiniensis* Froggatt, as described by Silvestri, Crampton and more recently by Browman. I have studied the ovipositor of *M. darwiniensis*

and agree with the above-mentioned authors that it bears a close resemblance to that of the BLATTIDAE.

An ovipositor is wanting in Embioptera and Zoraptera, according to Imms, Walker and Snodgrass, and it is not definitely known whether or not its rudiments make their appearance during development.

The genital ducts : The above studies of the development of the female ducts of Orthopteroid insects betray a process of specialisation which in some cases has taken place to a considerable extent within the same order.

In the Ephemeroptera the paired oviducts generally open separately behind the seventh sternum and there are no traces of a median oviduct nor that of a well-defined genital cavity. In some forms, like *Heptagenia*, *Siphlurus* and others, the terminal ends of the oviducts tend to approach each other, and the two oviducts open into a shallow genital cavity called the vestibule. The highest specialisation of the efferent system in Ephemeroptera is probably represented by that of *Habrophlebia fusca*, as described by Heiner, in which the paired oviducts open to the outside by a short median ectodermal passage probably formed by the modification of the vestibule.

The development of the female efferent system of the Dermaptera, except that of *Forficula auricularia*, is very imperfectly known. In *Forficula* an ectodermal invagination takes place behind the seventh sternum and forms the common oviduct. The spermatheca arises from the median invagination which takes place behind the eighth sternum.

The Plecoptera display a great amount of modification and specialisation of the female efferent system within the one order. In *Nemoura* and *Amphinemoura* the common oviduct opens behind the seventh sternum. In other forms, *e.g.*, *Chloroperla*, *Stenoperla* as shown above and in *Perla* and *Pteronarcys* as described by Schoenemund and Newport respectively, the female gonopore is situated behind the eighth sternum. The mode of posterior migration of the gonopore from the seventh to the hind margin of the eighth sternum has already been described in *Chloroperla*. In all the stoneflies studied, the spermatheca develops from a median invagination behind the eighth sternum, and this appears to be a general rule in Plecoptera.

In the Orthoptera typically three median invaginations take place in the hind abdominal region. The first behind the seventh sternum forms the common oviduct. The second behind the eighth gives rise to the spermatheca and the last invagination, which takes place behind the ninth sternum, gives rise to the female accessory glands, as shown in BLATTIDAE and TETTIGONIIDAE.

The position of the female gonopore of the adult is different in the various families of Orthoptera. In BLATTIDAE (probably also in MANTIDAE), GRYLLIDAE, and TETTIGONIIDAE the common oviduct opens between the seventh and eighth sterna at the base of a secondarily formed intersegmental subgenital plate. In ACRIDIDAE and also in PHASMIDAE, as described by Sinety (1901) and Chopard (1920), the gonopore of the adult female is located behind the eighth sternum. The posterior migration of the common oviduct from the hind margin of these venth sternum to that of the eighth has already been shown in ACRIDIDAE.

The development of the female ducts of Isoptera has been studied by Knower (1901), in *Termes flavipes*, and the adult morphology has been dealt with especially by Holmgren, Imms (1919) and more recently by Ahrens (1935). Knower's description shows practically the same mode of development in Isoptera as that occurring in *Blatta* and *Periplaneta*, and Ahrens has even located the female gonopore of Isoptera between the seventh and eighth sterna, as in the BLATTIDAE.

The development of the female ducts of Zoraptera has not been worked out and very little is known even about the morphology of the adult organs.

In Embioptera the development of the female efferent system has not been thoroughly worked out. The adult morphology of the female organs is, however, better known especially through the researches of Grassi and Sandias (1897–98), Verhoeff (1904), Imms (1913) and Mukerji (1927). According to the above-mentioned workers, the common oviduct opens on the eighth sternum in the adult. A spermatheca is also present in the Embiids and like that of the Orthoptera opens on the eighth segment.

From the above account it appears that among the Orthopteroid forms the primary position of the female gonopore is between the seventh and eighth sterna, from whence in some cases it migrates posteriorly during the post-embryonic development to open on the hind margin of the eighth sternum.

Among the Thysanura, a condition more or less similar to that of Orthoptera appears to exist, according to Ford (1923). The spermatheca and the common oviduct of *Lepisma*, *Japyx*, *Campodea* and others, open together behind the eighth sternum. In *Ctenolepisma quadriseriata* Pack., Ford states that the common oviduct opens between the seventh and eighth sterna, while the spermatheca opens between the eighth and ninth. This condition of *Ctenolepisma* probably represents a primitive condition and shows that a migration of the female gonopore from the hind margin of the seventh sternum to that of the eighth has taken place in Thysanura in a manner probably similar to that described in Plecoptera and Orthoptera.

So far as the primary position of the spermatheca is concerned Singh Pruthi, on the basis of his observations on the development of *Tenebrio molitor* (Coleoptera), remarks that the original position of the spermatheca lies between the ninth and tenth segments, and except in Coleoptera and Diptera it has lost its primary opening and communicates with the exterior by the opening of the uterus (common oviduct) on the eighth segment. George, in Hemiptera and Odonata, holds that the spermatheca may arise from any abdominal segment from the seventh to the ninth. According to Nel, Snodgrass and others the ancestral position of the spermatheca is on the eighth segment as represented by that of the Orthoptera.

My observations, however, suggest that the spermatheca has probably arisen with the development of the median ectodermal part of the efferent system in insects, and that the position of the spermatheca of *Heptagenia*, *Siphlurus* and other Ephemeroptera between the seventh and eighth sterna probably represents its most primitive condition. With the posterior migration of the female gonopore in insects carrying an ovipositor, the spermatheca develops from the invagination which takes place behind the eighth segment and lies between the bases of the anterior valves if the latter are present. Thus in most of the Exopterygota and many Endopterygota the spermatheca develops from the hind margin of the eighth segment. With the further posterior migration of the female gonopore to the hind margin of the ninth segment as found in Coleoptera and some Diptera, the spermatheca likewise acquires a position behind the ninth segment as shown by Singh Pruthi and Metcalfe. The development of a spermatheca on the hind margin of the seventh sternum in Trichoptera and in *Philaenus leucophthalmus* (Homoptera) as described by Dodson and George respectively probably recapitulates the ancestral position of the spermatheca on the seventh segment, while that of the Coleoptera and *Dasyneura* (Diptera) represents the highest specialisation.

B. The male.

The genitalia: The morphology of the male genitalia of Orthopteroid insects including Ephemeroptera, Dermaptera, Plecoptera and Orthoptera has been discussed above.

A brief comparison of the penes of Ephemeroptera and Dermaptera with the penis valves of Orthoptera is called for here. The penes of both the mayflies and the earwigs, as well as the penis valves of Orthoptera and Plecoptera, develop as a pair of outgrowths from the wall of the genital cavity behind the ninth segment. In Ephemeroptera and Dermaptera the penes are, however, traversed by the paired ejaculatory ducts. Their homology with the penis valves of Orthoptera, therefore, requires some consideration. It has already been shown above that the penes of Ephemeroptera and Dermaptera, like the penis valves of Orthoptera and Plecoptera, appertain to the tenth segment and have also been regarded as appendicular in nature. It may, therefore, be assumed that the penis valves of Orthoptera and the penes of Ephemeroptera and of Dermaptera, if not differently modified homologous structures, are, however, very closely related in their nature.

It may also be pointed out that Snodgrass (1936–37) in his recent works concludes that the inner part of the male genitalia of various families of the Orthoptera develops without a fundamentally common plan. This conclusion receives no support from the present observations. It has already been shown above that in Blattidae, Tettigoniidae, Gryllidae and Acrididae the various parts of the penis valves of the adult arise from a single pair of ectodermal outgrowths of the base of the genital cavity. Chopard's observations on *Pholidoptera femorata* (Tettigoniidae) and those of Walker on *Grylloblatta campodeiformis* (Grylloblattidae) point towards the same fact. It seems, therefore, that throughout Orthoptera the inner genital structure of the adult develops from the modification of a single pair of penis valves arising from the base of the genital cavity.

In Isoptera and Embioptera the inner part of the male genitalia is highly reduced. In the former, the presence of a pair of styli borne on the ninth sternum of *Mastotermes darwiniensis* strongly points out the close affinities of Isoptera with Blattidae.

In Zoraptera, Crampton, Walker and Snodgrass describe the presence of a pair of lobes which form the inner part of the male genitalia. Walker has termed them dextral and sinistral parameres while Snodgrass calls them right and left phallomeres. They seem to represent the paired penis valves of Orthoptera, and it appears that their differentiation into dorsal and ventral parts has not been well marked as in the penis valves of Orthoptera.

The development of the male genitalia of various insects has been differently interpreted. Singh Pruthi (Homoptera and Coleoptera), George (Homoptera) and Metcalfe (Homoptera and Coleoptera) have adopted the view held by Crampton and Walker for Orthoptera, and have regarded the primary rudiments of the male organ as the endopodites of the ninth abdominal appendages. They have homologised them with the posterior ovipositor valves of the female. According to the other view, represented by the " stilplan " of Zander, the paired rudiments of the male genitalia are special outgrowths of the body-wall and are not homologous with the posterior valves. The same view holds that each of these primary rudiments (primitivzapfen) divides into a lateral and a median part. The median parts of the two sides fuse to form the valvae of median intromittent organ, while the lateral parts form the valves, harpes or

the clasping organs of the male. The above-mentioned view has been adopted by Kerschner for Coleoptera, by Christophers for Hemiptera and Diptera and by Boulangé for Hymenoptera.

Mention should also be made of the view, which regards the copulatory organ of Insecta as a median outgrowth of the body-wall posterior to the ninth segment. This view, which was held by Sharp and Muir for Coleoptera, has recently been adopted by Snodgrass for the median copulatory organ of the insects in general, and a reference to his theory of the origin of the male genitalia as phallic and periphallic structures has already been made.

A final theory, at first adopted by Huxley and recently revived by Else, Roonwal, Sharif and Rawat, maintains that the inner parts of the male genitalia of insects arise from the appendages of the tenth segment.

As regards the first-mentioned view of Crampton, Walker, Singh Pruthi, George and Metcalfe, it has been shown previously that it receives no support from the development of Orthopteroid insects. In other insects, the observations of Mehta in Lepidoptera, of Sharif in Aphaniptera and of Rawat in Hemiptera–Heteroptera, have clearly shown that the primary rudiments of the intromittent organ do not develop in connection with the appendages of the ninth segment.

The second view held by Zander has received a fairly wide support from the development of insects, so far as the paired origin of the median intromittent organ is concerned. It is, however, doubtful whether the development of the lateral structures of the male genitalia is in all cases in accord with the findings of Zander. The various lateral structures of the male genitalia have been differently termed parameres, valvae, harpes, subgenital plates or harpagones. They probably fall into two groups. The first group consists of the structures which arise by the division of the primary paired rudiments of the copulatory organ and are comparable with the parameres of Dermaptera. The other develops from the ninth segment and appear to be homologous with the styli of Orthoptera or with the claspers of Ephemeroptera. The identification of these two kinds of structures requires a careful study of development, and Mehta's researches have shown that in Lepidoptera the valvae develop independently of the penis lobes and not by their division into two as claimed by Zander. A similar doubt on the nature of the lateral processes of the male genitalia of Hymenoptera has arisen owing to the recent researches of Peck (1938), and he regards the squamae of Hymenoptera as comparable with the valvae of Lepidoptera and the harpagones of Mecoptera. Thus it is possible that further researches on development may prove that the squamae of Hymenoptera are not developed from the division of penis lobes as described by Zander but arise independently of them like the valvae of Lepidoptera as shown by Mehta.

The parameres of Coleoptera, Hemiptera and Aphaniptera appear to arise by the division of the primary rudiments of the copulatory organ and are homologous with the parameres of Dermaptera. The researches of Singh Pruthi in Coleoptera, of Sharif in Aphaniptera and of Rawat in Hemiptera–Heteroptera have shown them to develop independently of the appendages of the ninth segment.

So far as the unpaired origin of the copulatory organ is concerned, my observations, as well as those mentioned above, clearly point to the contrary. It may definitely be stated that Snodgrass' theory of the median and unpaired origin of the phallus (copulatory organ) does not receive support from the development of insects. Snodgrass derives the phallus of the Pterygota from

the penis of Thysanura, which according to him is a median outgrowth of the body-wall behind the ninth segment. The development of the penis of Thysanura is very imperfectly known. Crampton, however, describes a bipartite penis in *Nicoletia* (Lepismidae). I have cut sections of very young nymphs of *Machilis maritima* and my preparations clearly show that in *Machilis* the penis is formed by the fusion of a pair of outgrowths of the genital cavity probably comparable with the penis valves of Orthoptera, and also show that the latter (penis valves) develop independently of the parameres (gonapophyses) of the ninth segment (pl. 7, figs. 52, 53 & 54).

It is, therefore, very probable that the male genitalia of Pterygota have been evolved from a common basic plan. The structures, which are variously termed subgenital plates, valvae, harpes and harpagones, represent the appendages of the ninth segment and are comparable with the styli of Thysanura, Ephemeroptera and Orthoptera borne on the coxites of the ninth segment. The median aedeagus and parameres, on the other hand, develop from a pair of lobes termed variously " primitivzapfen," paramere lobes, penis lobes or phallomeres, and these paired rudiments of the inner part of the male genitalia appear to be homologous with the penis valves of Orthoptera previously described.

Regarding the nature and homology of these primary rudiments of the copulatory organ, reference has already been made to the findings of Else, Sharif and Rawat, and it appears that they probably represent the appendicular outgrowths of the tenth abdominal segment which have moved medially and anteriorly, apparently owing to the formation of the genital cavity.

The genital ducts : The development of the male ducts of Ephemeroptera, Dermaptera, Plecoptera and Orthoptera has been described above. It has been shown that in all of them the *vasa deferentia* extend to the hind margin of the ninth segment, where they end as terminal ampullae. In the case of Ephemeroptera and Dermaptera, the paired ectodermal invaginations of the apices of the penes form the paired ejaculatory ducts which later communicate with the ampullae of the *vasa deferentia.* In Ephemeroptera the male ducts are paired from end to end, while in Dermaptera, excepting *Anisolabis*, the paired ejaculatory ducts unite anteriorly and the common duct thus formed communicates with a single vesicula seminalis formed by the fusion of the ampullae of the *vasa deferentia.* In Plecoptera and Orthoptera a median invagination takes place between the bases of the penis valves, and forms the median ejaculatory duct. The terminal ampullae of the *vasa deferentia* open into its anterior end.

It may be pointed out that the paired ejaculatory ducts of Ephemeroptera and Dermaptera are not homologous with the median ejaculatory duct of Orthoptera and other insects. Nor can even the single ejaculatory duct of *Forficula auricularia*, which results by the suppression of the other ejaculatory duct, be compared with the median ejaculatory duct of the former. In Orthoptera and other higher Pterygota the paired ejaculatory ducts have been lost altogether, and the median ejaculatory duct develops as an entirely different structure.

In Isoptera, Knower has studied the development of the genital ducts of *Termes flavipes.* His findings show that the male genital ducts of *Termes* develop in a corresponding manner to those of Blattidae and other Orthoptera, and his conclusions are in entire agreement with those of Wheeler and Heymons.

Very little is known about the development of the male ducts of Embioptera and Zoraptera. The morphology of the adult organs, however, suggests

their resemblance with those of Plecoptera and Orthoptera, as shown by Snodgrass.

One of the main views which has crystallised out following the researches of Wheeler and Heymons in Orthoptera, regards the median ejaculatory duct as alone representing the ectodermal part of the male efferent system, while the *vasa deferentia* and their terminal ampullae which give rise to the male accessory glands are mesodermal in origin. My observations on the development of Orthopteroid insects are in agreement with this view, which recently has also been supported in Orthoptera by Else, Roonwal and Snodgrass. Among the other insects, a number of workers, including especially Knower in Isoptera, George in Odonata and Homoptera, Christophers and Cragg, and Rawat in Heteroptera, Zander in Hymenoptera, Verson and Bisson, and Zick in Lepidoptera, Kerschner in Coleoptera, Christophers and Lowne in Diptera, hold the same view as regards the nature of the various parts of the efferent system, as stated in Orthoptera.

The other view, which is probably derived from the conclusions of Nussbaum, has recently been especially upheld by Singh Pruthi (Homoptera and Coleoptera), Metcalfe (Homoptera and Coleoptera), Mehta (Lepidoptera), and Sharif (Aphaniptera). The above-mentioned authors regard the posterior terminal ends of the *vasa deferentia* and the male accessory glands as ectodermal in nature, since according to them they arise from a pair of ejaculatory ducts which posteriorly communicate with the median ejaculatory duct and anteriorly with the *vasa deferentia*. From their description, it appears that the above workers interpret the terminal ampullae of the *vasa deferentia* as ectodermal. It is difficult for me to speak definitely regarding the nature of the terminal ampullae of all insects, since embryological researches are wanting in a number of various orders. So far as Orthoptera are concerned, the recent embryological researches of Else and Roonwal give strong support to the observations of Wheeler and Heymons and show that the terminal ampullae are the remnants of the embryonic coelomic pouches of the tenth abdominal segment. Thus the distal ends of the *vasa deferentia* and the male accessory glands of Orthoptera should be regarded as mesodermal structures.

VII. Summary.

The development of the male and female genitalia and their ducts has been studied in Ephemeroptera, Dermaptera, Plecoptera and Orthoptera.

In Ephemeroptera no traces of an ovipositor are present. The paired oviducts directly open behind the seventh sternum. The penes develop independently of the claspers and probably belong to the tenth segment. Neither penes nor their accessory processes represent the parameres of Thysanura or other Pterygota. The basal segment of the clasper alone represents the coxite of the ninth segment; the remaining segments represent secondary divisions of the stylus. The *vasa deferentia* open outside through paired ectodermal ejaculatory ducts.

In *Forficula auricularia* (Dermaptera) no traces of an ovipositor appear. Paired penis lobes develop behind the ninth segment and correspond to those of Ephemeroptera. The parameres arise by the division of the penis lobes. A median penis in adult *Forficula* is formed by the reduction of one penis. In *Hemimerus* both penes fuse together. Paired ectodermal ejaculatory ducts develop as in Ephemeroptera.

In Plecoptera rudimentary anterior valves appear during development.

In Nemouridae the female gonopore is situated behind the seventh sternum. In Perlidae it has migrated behind the eighth. In *Chloroperla* an eversible penis is formed by paired penis valves, as in the Orthoptera.

In Orthoptera the anterior ovipositor valves are neither homologous with the posterior nor the lateral valves, but are probably homologous with the styli of the eighth segment of the Thysanura. The female gonopore is situated behind the seventh segment in Blattidae, Tettigoniidae and Gryllidae and behind the eighth in Acrididae. In the male, paired penis valves common to all Orthoptera probably represent appendicular outgrowths of the tenth segment. They divide into ventral and dorsal parts which surround the gonopore. The ejaculatory duct belongs to the tenth segment. The male accessory glands are mesodermal.

A review of development shows that the male copulatory organ of insects does not develop as a median outgrowth, as supposed by Snodgrass, but arises from paired rudiments. In *Machilis* the penis is shown to develop from paired lobes, independently of the gonapophyses of the ninth segment.

VIII. Literature.

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IX. Explanation of the Lettering Used on the Plates.

ag–ap, aperture of the accessory glands.
agin, invagination of the accessory glands.
amp, ampullae.
bc, bursa copulatrix.
c, coxite.
cod, common oviduct.
codin, invagination of the common oviduct.
dpnv, dorsal penis valves.
ejd, ejaculatory duct.
ejdin, invagination of the ejaculatory duct.
ep, epigynum.
gc, genital cavity.
ldpnv, left dorsal penis valve.
lvpnv, left ventral penis valve.
lejd, left ejaculatory duct.
lpn, left penis.
mclcl, muscles of the clasper.
ng, nerve ganglion.
od, oviduct.
odamp, ampullae of the oviduct.
pm, parameres.
pn, penis.
pnv, penis valves.
rdpnv, right dorsal penis valves.
s, sternum.
sgp, subgenital plate.
spap, spermathecal aperture.
spin, invagination of the spermatheca.
spr, spermatheca.
sty, stylus.
vd, vas deferens.
vl, ovipositor valves.
vlf, valvifer.
vpnv, ventral penis valves.

Plate 1.

Fig. 1. Transverse section through the seventh abdominal segment of a female nymph of *Heptagenia* sp., 5·5 mm. long.
2. Horizontal section through the abdomen of a fully developed female nymph of *Ephemera vulgata*.
3. Transverse section passing through the terminal abdominal region of a young male nymph of *Rhithrogena* sp., 3·5 mm. long.
4. Transverse section passing through the ninth segment of a young male nymph of *Rhithrogena* sp., 3·5 mm. long.
5. Transverse section passing through the penis of a male nymph of *Heptagenia* sp., 8 mm. long, showing the formation of the ejaculatory ducts.
6. Same, more towards the anterior end.
7. Transverse section passing through the penis of a male nymph of *Heptagenia* sp., 10 mm. long.
8. Transverse section passing through the ampullae of the *vasa deferentia* of a male nymph of *Heptagenia* sp., 10 mm. long.

PLATE 2.

FIG. 9. Transverse section passing through the hind abdominal region of the first instar male nymph of *Forficula auricularia*.
10. Transverse section passing through the terminal end of the abdomen of the first instar male nymph of *Forficula auricularia*.
11. Transverse section passing through the penes of the second instar male of nymphs of *Forficula auricularia*.
12. Same, a few sections towards the anterior end.
13. Transverse section passing through the penes of the third instar male nymphs of *Forficula auricularia*.
14. Same, a few sections towards the anterior, showing the fusion of the ejaculatory ducts.
15. Same, a few sections towards the anterior end.

PLATE 3.

FIG. 16. Transverse section passing through the eighth segment of a female nymph of *Nemoura variegata* 6 mm. long.
17. Longitudinal section passing through the abdomen of a female nymph of *N. variegata*, 8·5 mm. long.
18. Longitudinal section of a full-grown female nymph of *Chloroperla* sp., showing the common oviduct.
19. Transverse section passing through the seventh segment of a female nymph of *Amphinemoura* sp., 5 mm. long.
20. Longitudinal section passing through the abdomen of a young male nymph of *Amphinemoura* sp., 5 mm. long.
21. Transverse section passing through the terminal part of the abdomen of a male nymph of *Chloroperla*, 9 mm. long.
22. A few sections more towards the anterior end.
23. Longitudinal section passing through the abdomen of a male nymph of *Chloroperla* sp., 8 mm. long.

PLATE 4.

FIG. 24. Transverse section passing through the eighth segment of the first instar female nymph of *Blatta orientalis*.
25. Transverse section passing through the terminal part of the abdomen of a young fourth instar female nymph of *B. orientalis*.
26. Transverse section passing through the seventh segment of a first instar female nymph of *B. orientalis*.
27. Transverse section passing through the seventh segment of a fourth instar female nymph of *B. orientalis*.
28. Longitudinal section passing through the abdomen of a first instar male nymph of *B. orientalis*.
29. Transverse section passing through the abdomen of a first instar male nymph of *B. orientalis*.
30. Transverse section passing through the hind end of the abdomen of a third instar male nymph of *B. orientalis*.
31. Transverse section passing through the hind end of a first instar male nymph of *B. orientalis*.

PLATE 5.

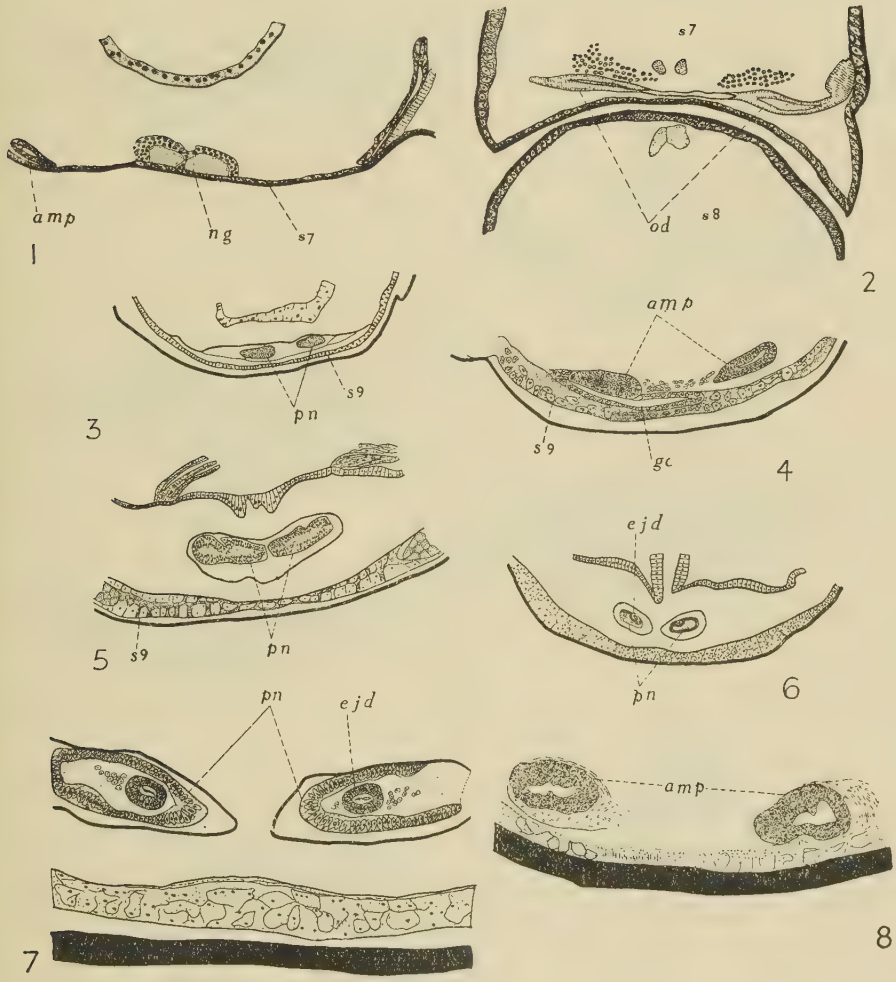
FIG. 32. Transverse section passing through the abdomen of a female nymph of *B. orientalis* about 10 mm. long.
33. Transverse section passing through the seventh segment of a penultimate nymphal instar of *Leptophyes punctatissima.*
34. Transverse section of the male genitalia of nymph of *L. punctatissima,* one instar older than that in fig. 50.
35. Same, a few sections towards the anterior end.
36. Transverse section of the same nymph as in Fig. 50, a few sections towards the anterior end.
37. Transverse section of a well-grown male nymph of *L. punctatissima* about 10 mm. long.

PLATE 6.

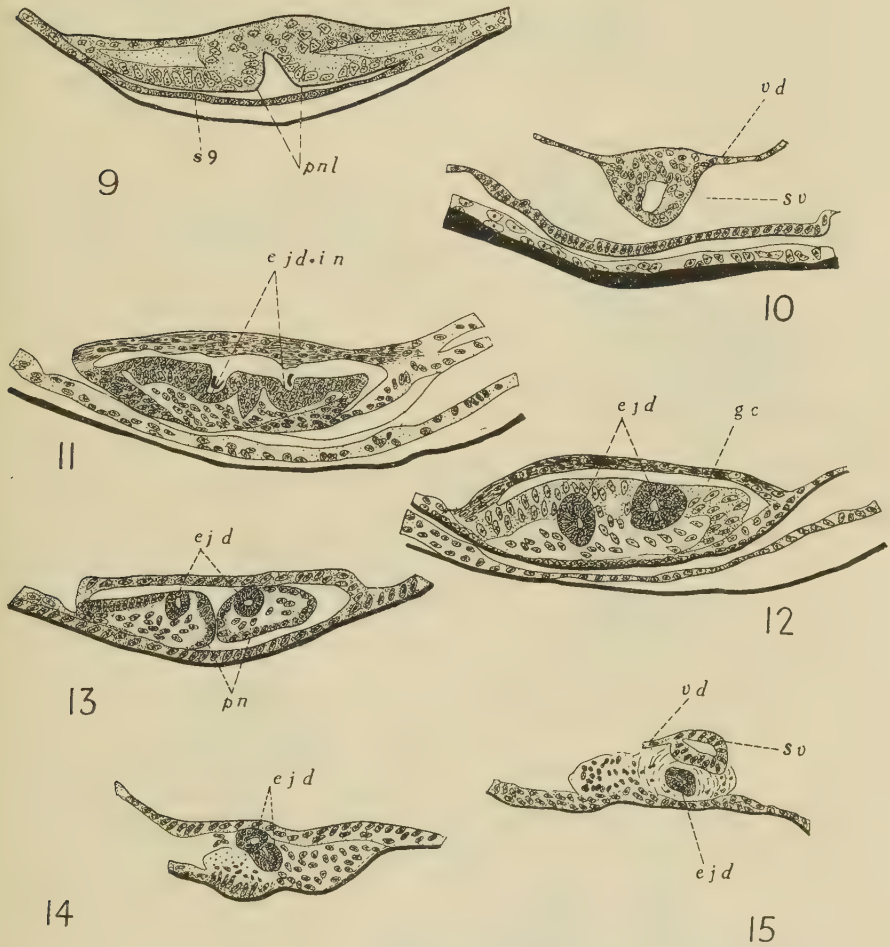
FIG. 38. Transverse section passing through the eighth segment of a full-grown second instar female nymph of *Gryllulus domesticus.*
39. Transverse section passing through the terminal end of the abdomen of a second instar female nymph of *G. domesticus.*
40. Transverse section passing through the abdomen of a second instar female nymph of *G. domesticus.*
41. Transverse section passing through the abdomen of a third instar female nymph of *G. domesticus.*
42. Transverse section passing through the abdomen of a first instar male nymph of *G. domesticus.*
43. Transverse section passing through the terminal end of the abdomen of a first instar male nymph of *G. domesticus.*
44. Transverse section passing through the abdomen of a fourth instar male nymph of *G. domesticus.*

PLATE 7.

FIG. 45. Transverse section passing through the eighth segment of the second instar female nymph of *Locusta.*
46. Transverse section passing through the lateral valves of the first instar nymph of *Locusta.*
47. Same, a few sections towards the anterior end.
48. Transverse section passing through the seventh segment of the first instar of *Locusta.*
49. Longitudinal section passing through the abdomen of the second instar female nymph of *Locusta.*
50. Transverse section passing through the abdomen of the fifth instar male nymph of *Locusta.*
51. Transverse section passing through the hind end of the abdomen of first instar male nymph of *Locusta.*
52. Transverse section passing through the terminal end of the abdomen of a very young nymph of *Machilis maritima.*
53. Same, a few sections towards the anterior end.
54. Same, a few sections more towards the anterior end.



Qadri: Development of Genitalia in Orthoptera.



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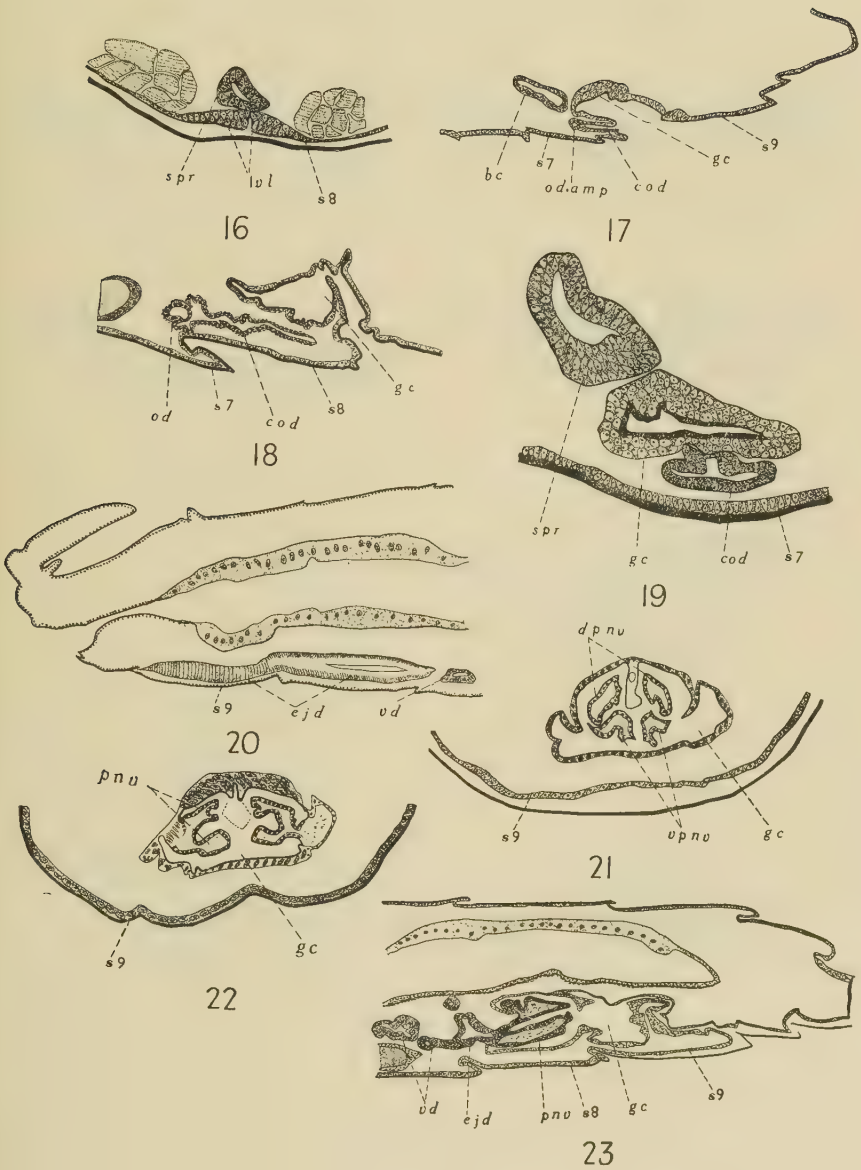

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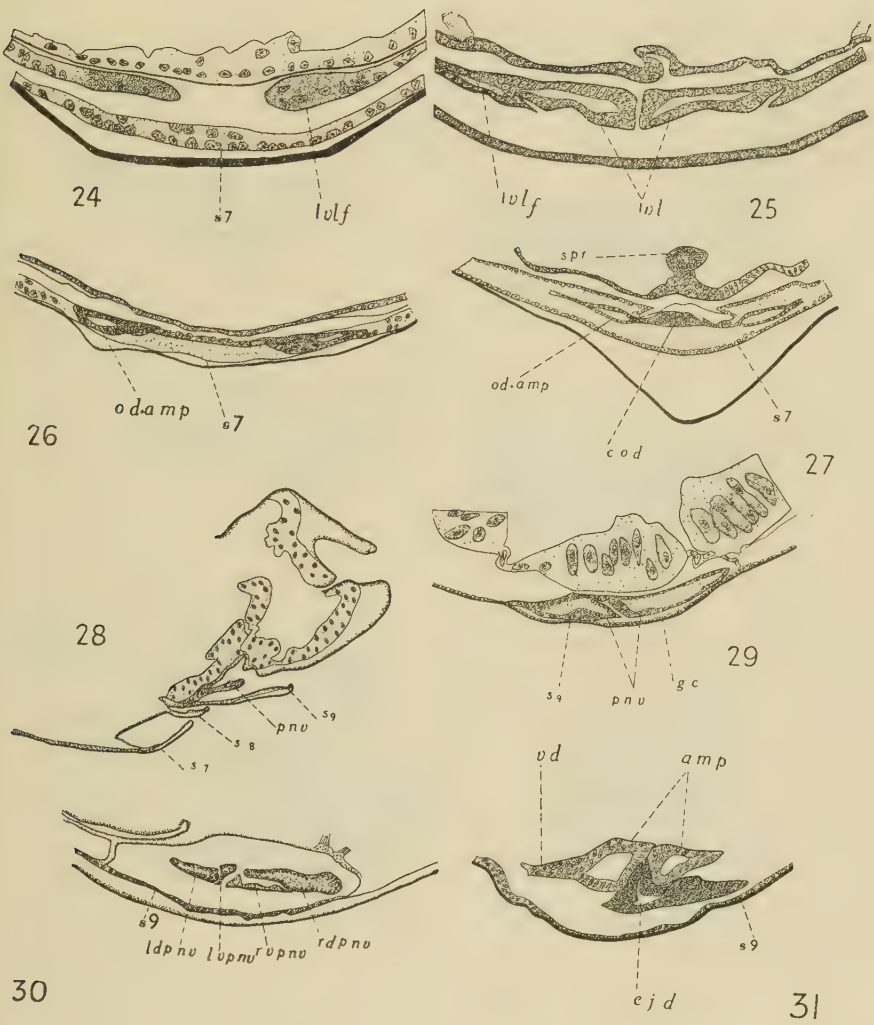

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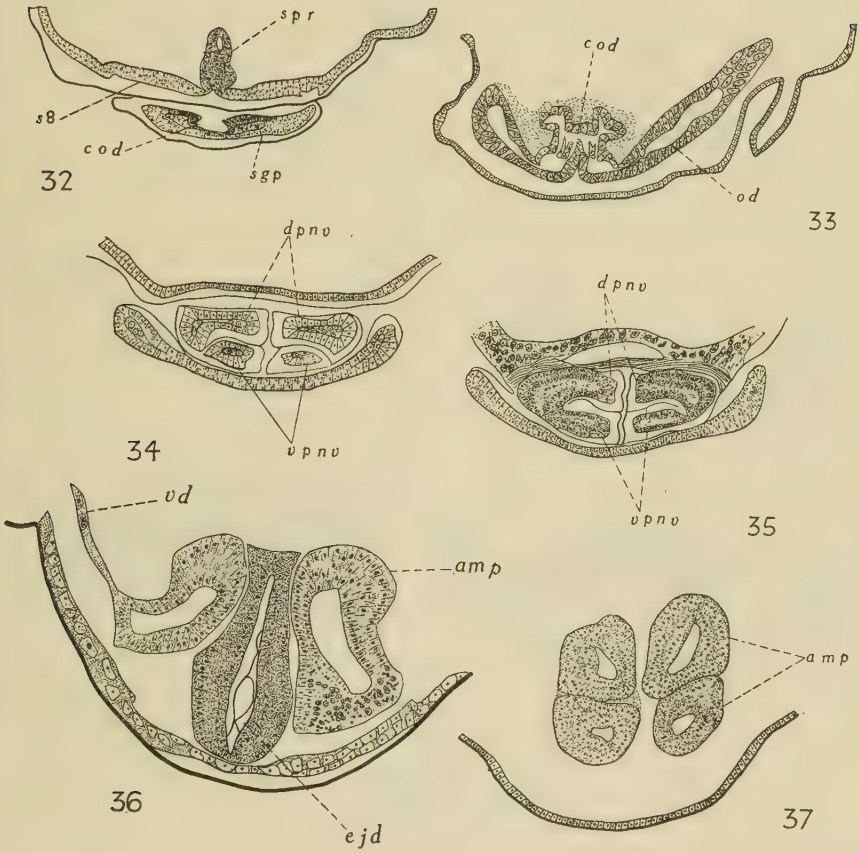

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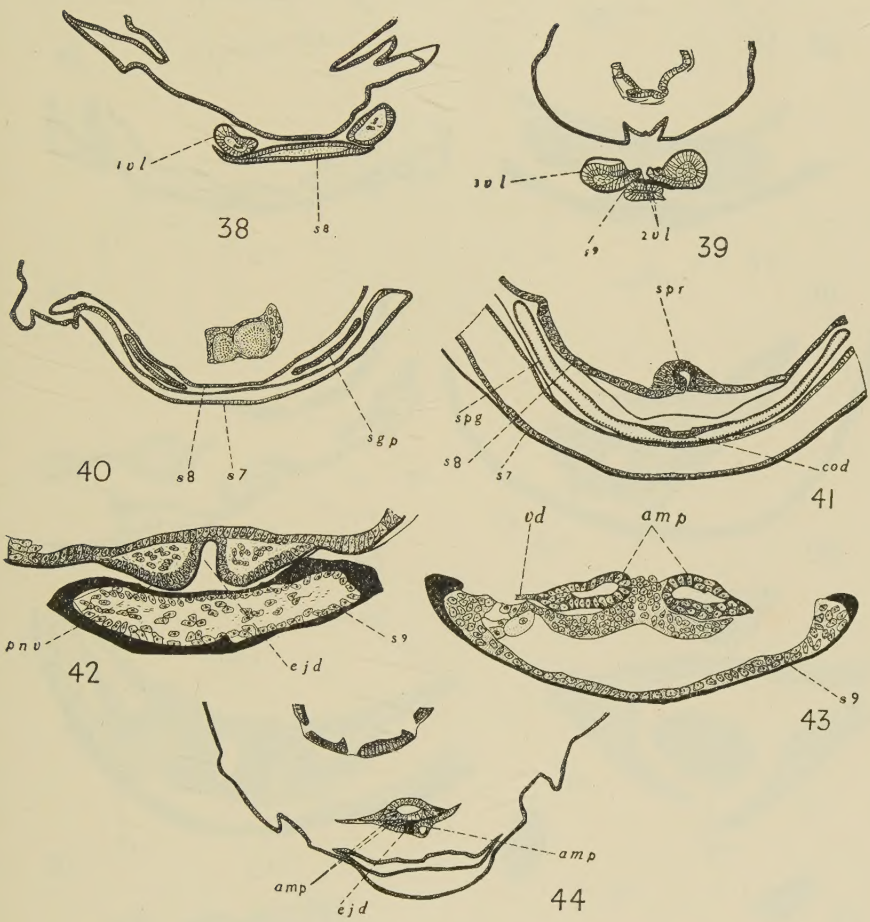

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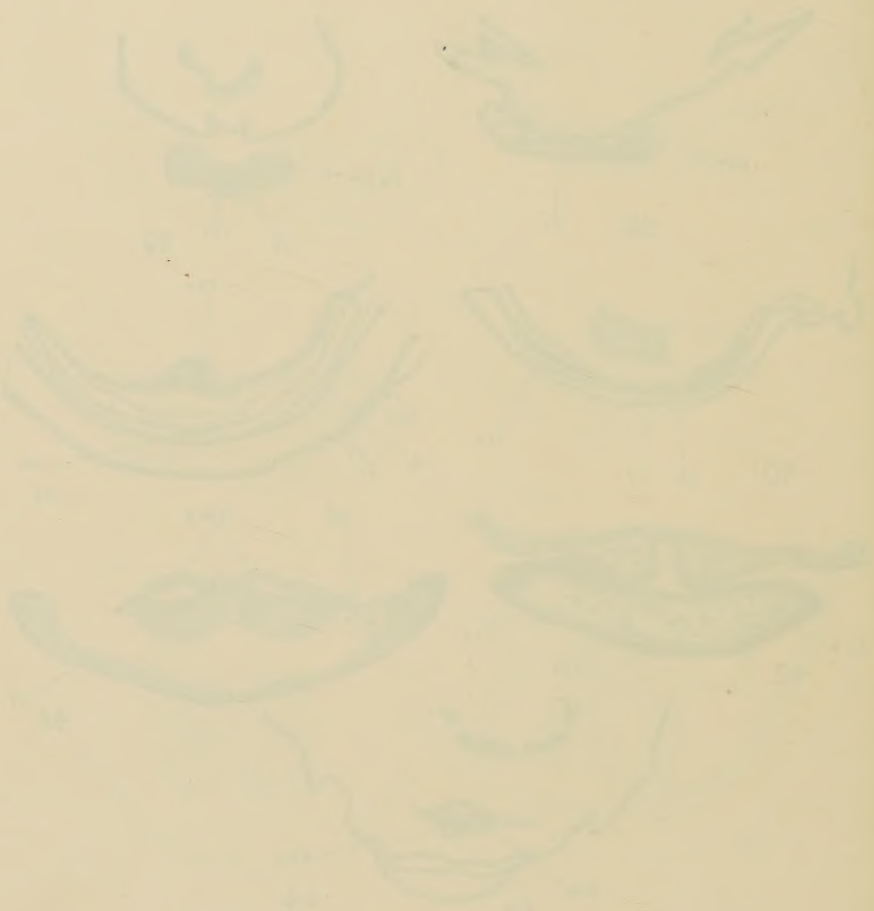

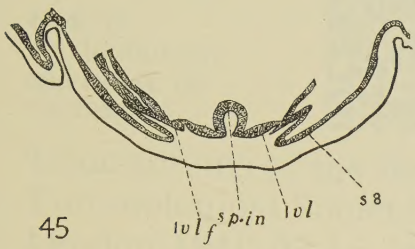

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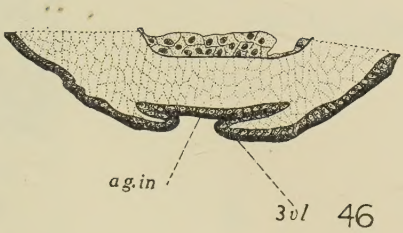

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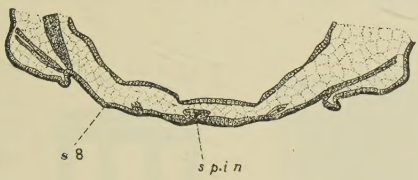

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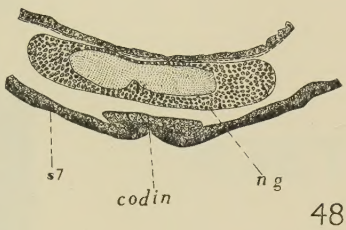

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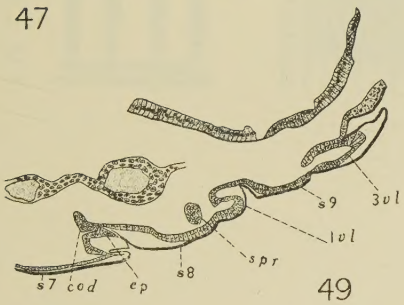

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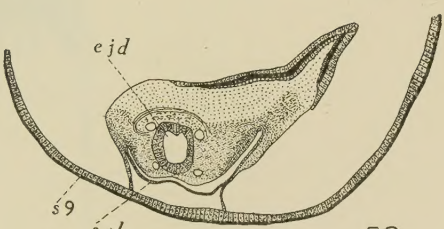

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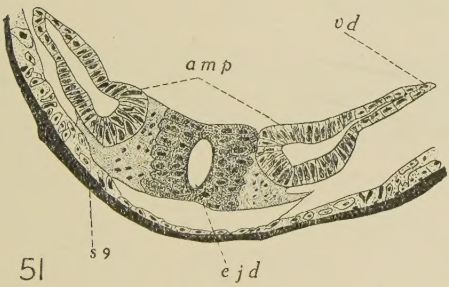

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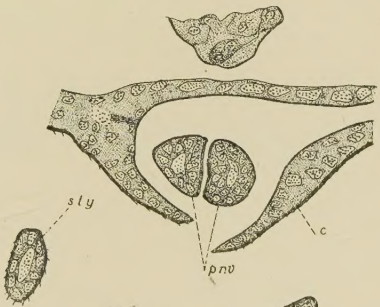

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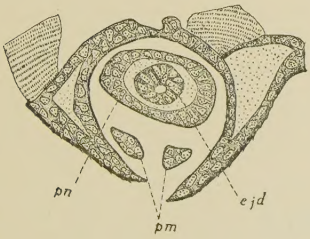

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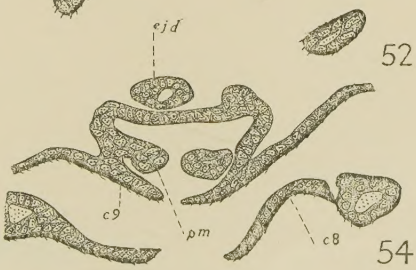

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